AGRICULTURAL BOTANY

Gill & Vear

2. Monocotyledonous Crops

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Third Edition, revised by

K. C. Vear and D. J. Barnard

2. MONOCOTYLEDONOUS CROPS

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PREFACE

As explained in the preface to Volume I it was decided that this new edition of *Agricultural Botany* would be most appropriately issued as a series of separate volumes. The present volume covers the ground of chapters fourteen to seventeen of the earlier editions, with the addition of a brief discussion of the general characters and structure of the monocotyledons, and with some expansion of the treatment of families other than the grass family. This has however been kept to a minimum and no attempt has been made to deal in detail with tropical monocotyledonous crops, or with the full range of monocotyledonous ornamentals grown in Britain. In the account of the *Gramineae*, which forms the major part of the volume, the separate treatment of cereals and herbage grasses has been retained, as being more convenient from a teaching point of view than a strictly taxonomic arrangement.

The work has been revised throughout, and many sections largely rewritten in an attempt to take account of advances in knowledge, alterations in interpretation and nomenclature, and changes in agricultural practice since the last edition; the adoption of E.E.C. regulations and of metrication have also necessitated substantial changes. The rapidity with which new cultivars of cereals and herbage grasses come into use and older ones disappear makes it impossible for a book of this type to remain up-to-date. We have therefore tried to place emphasis on the general range of forms and on the trends observable, rather than on a detailed description of cultivars in use at the time of writing, referring the student to current literature, and in particular to the frequently revised publications of the National Institute of Agricultural Botany, for up-to-date information.

K.C.V.
D.J.B.

1

MONOCOTYLEDONS: GENERAL CHARACTERS

The angiosperms, flowering plants in which the seed is formed inside a closed ovary, are divisible into two groups, the dicotyledons and the monocotyledons. The former is the larger, with some 240 families including perhaps 240 000 species, compared with the 45 families and 50 000 species of the monocotyledons.

From the point of view of crop plants, one monocotyledonous family is of outstanding importance. This is the *Gramineae,* which includes the cereals and the herbage grasses. Since these two types of crop provide, in most parts of the world, the main constituents of the diet of human beings and of domesticated animals, crops belonging to this one family far outweigh those of all other families in agricultural importance. In Britain crops belonging to the *Gramineae* occupy some 90% of the total cultivated area, and the same sort of proportion holds in most temperate regions; the greater part of this volume is therefore devoted to this one family. Other monocotyledonous families are, in comparison, of relatively minor importance in temperate regions, although they provide some major tropical crops.

Macroscopic characters

The primary character separating the monocotyledons from the dicotyledons is of course the structure of the embryo, with one cotyledon only instead of two. There are however many other and more conspicuous differences; it is difficult to find any absolute criterion which is always applicable, but in most cases monocotyledons are readily distinguishable from dicotyledons. Some of the more important features may be summarized as follows:

Stems. Aerial stems in monocotyledons are usually annual herbaceous structures; only in a limited number of cases do such stems become woody. In plants living for more than one year some form of shortened perennating stem, usually underground, is common; this may be a rhizome, tuber or corm, or may form the base of a bulb.

Roots. Usually short-lived structures, often adventitious from the nodes of the stem.

Leaves. Typically narrow, parallel veined, usually alternate. Sheathing bases are common, often swollen and persisting to form perennating bulbs.

Flowers. Most commonly actinomorphic, with parts almost always in threes; typically a perianth of 3 or 3 + 3 segments, often conspicuous and petalloid where the flower is insect pollinated, small or absent in wind pollinated species, stamens 3 or 3 + 3, carpels usually 3, united, superior or inferior.

Fruit. Often a capsule, and then usually trilocular, either loculicidal or septicidal; sometimes a berry, which may be one or more seeded. The fruit in most grasses is a caryopsis, with the very thin pericarp adherent to the testa of the single seed.

Seed. Usually endospermic, with a relatively small embryo.

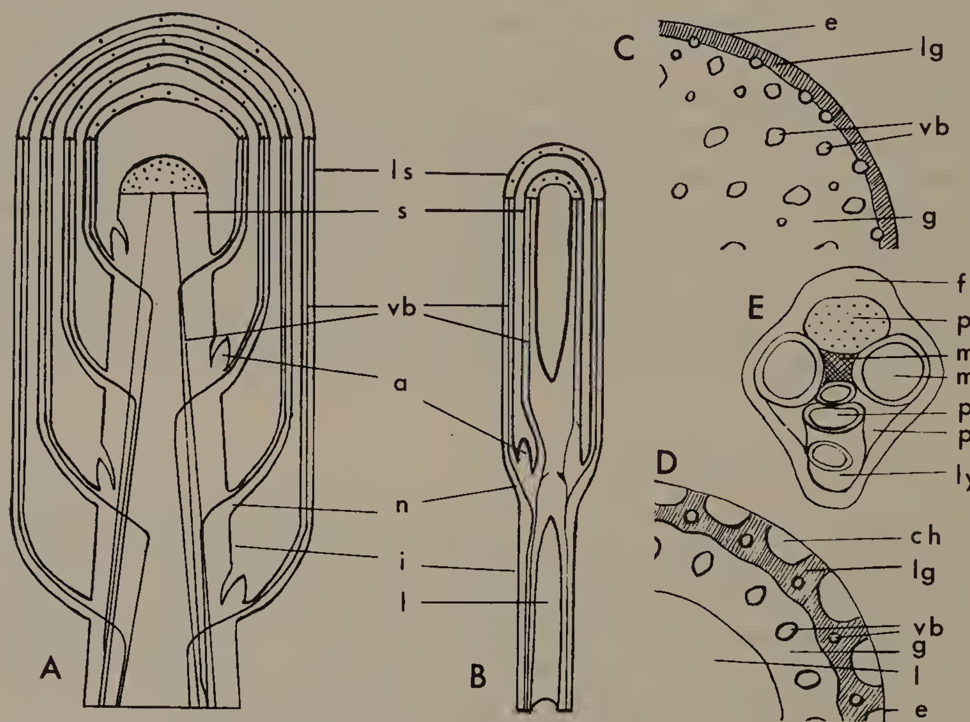


Fig. 1. Structure of monocotyledonous stems. A, diagrammatic view of part of shoot of solid-stemmed grass cut lengthwise; B, of hollow-stemmed type, through one node only. C, part of transverse section through internode of a solid stem; D, of a hollow stem. E, transverse section of a single vascular bundle. *a,* axillary bud; *ch,* chlorenchyma; *e,* epidermis; *f,* fibres of bundle sheath; *g,* ground tissue parenchyma; *i,* internode; *l,* lumen; *lg,* lignified ground tissue; *ls,* leaf sheath; *ly,* lysigenous cavity; *mt,* metaxylem tracheids; *mv,* metaxylem vessel; *n,* node; *p,* parenchyma; *ph,* phloem; *pt,* protoxylem; *s,* stem; *vb,* vascular bundle. Not to scale.

Microscopic structure

Stem. Vascular bundles differentiate from procambial strands as in dicotyledons. They are not however arranged in a single ring but follow a sinuous path so that in the internodes of a solid stem they appear scattered throughout the parenchyma. There is thus no distinction of the latter into pith and cortex as there is in a dicotyledonous stem, and it is usually referred to as *ground tissue.* It is bounded on the outside by the single-layered epidermis, which consists usually of cells which are approximately rectangular in outline and elongated in the direction of the stem axis, rather than irregular, jigsaw-like as in dicotyledons. Stomata are present, more regularly arranged than in dicotyledons, and developing in such a way that each pair of guard-cells is surrounded by a pair of *accessory cells.*

Vascular bundles tend to be uniform in structure throughout the group. A small number of protoxylem cells differentiate on the side of the procambial strand nearest to the centre of the stem; these are followed by a rather larger number of tracheids of the metaxylem, and these are flanked by two large pitted vessels. Adjacent to the metaxylem the cells differentiate as phloem cells, similar to those of dicotyledons but more regularly arranged with alternating sieve-tube elements and companion cells. No cambium is present, and each vascular bundle is typically surrounded by a single or double layered *bundle sheath,* which may be lignified. In some monocotyledonous stems, as for example in the aerial stems of most grasses, the internodes are hollow at maturity. In these the vascular bundles are not scattered throughout the whole cross-sectional area, but are confined to the outer part, where they form two rather irregular rings. The central part of the stem is composed of parenchymatous ground tissue only, and this breaks down to leave a central cavity or *lumen.* The nodes are solid, with a complex network of more or less horizontally arranged bundles.

Since there is no cambium, no normal secondary thickening takes place. Mechanical strength, where this is necessary, is provided, not by the small amount of lignified xylem tissue present in the bundles, but by lignification of the bundle sheaths, or of part or the whole of the ground tissue, as for instance in some palms and bamboos, where there is an elongated perennial aerial stem. In *Dracaena* and a few related woody-stemmed genera of the *Liliaceae* a special type of cambium arises in the ground tissue under the epidermis, and gives rise not to separate layers of secondary xylem and phloem, but to whole new secondary bundles of the same form as the primary ones, and separated by new secondary ground tissue.

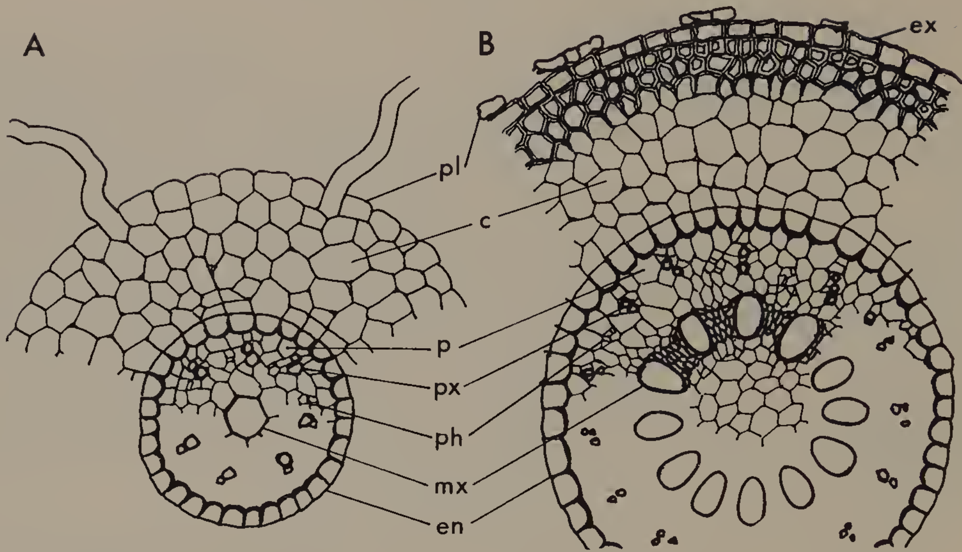


Fig. 2. Transverse sections of monocotyledonous roots. A, small grass root in young stage with functional root-hairs, seven protoxylem groups and single central metaxylem element, × *c.* 150. B, large grass root in older stage with piliferous layer largely lost and outer cortex sclerotized, polyarch, with metaxylem elements in ring surrounding central parenchyma, × *c.* 100. *c,* cortex; *en,* endodermis; *ex,* exodermis; *mx,* metaxylem; *p,* pericycle; *ph,* phloem; *pl,* piliferous layer; *px,* protoxylem.

Root. The internal structure is similar to the primary structure of dicotyledonous roots, except that it is frequently polyarch, that is there are numerous protoxylem groups, and these often surround a considerable central area of parenchyma; the metaxylem elements tend also to be less regularly arranged, and not confined to the same radii as the protoxylem cells. In addition, the endodermis is often more conspicuous than in dicotyledons, with its cells thickened on their inside as well as their radial walls. No secondary thickening takes place and the cortex is not sloughed off. In older roots, however, the piliferous layer may be lost and the subepidermal cells developed as a protective layer: the *exodermis*; the outer cortex may also become lignified.

Leaf. The leaf is not commonly markedly dorsiventral; it usually shows vascular bundles similar in structure to those of the stem surrounded by relatively undifferentiated mesophyll. Mechanical strength is often provided by strands of sclerenchyma surrounding the bundles or elsewhere. The epidermis is often similar to that of the stem, with stomata arranged in regular lines; it may show, as in the upper epidermis of grass leaf-blades, a considerable range of cell type.

2

CROP PLANTS: FAMILIES OTHER THAN GRAMINEAE

LILIACEAE

General importance. Contains numerous ornamental plants, but only one genus important as food-crops, the onions and related plants.

Botanical characters. Mainly herbaceous plants, often bulbous. Leaves alternate, often sheathing at the base. Inflorescence usually a raceme; an umbel only in *Allium* and related plants.* Flowers actinomorphic, usually insect-pollinated, with a perianth of six usually petaloid segments, six stamens, and a superior gynaecium of three united carpels. Placentation axile; fruit a capsule or berry; seeds usually numerous, endospermic. (For floral diagram see Fig. 3, A.)

Allium cepa L. **Onion**

A bulbous plant, behaving usually as a biennial. Stem in vegetative condition very short, conical, bearing numerous distichously-arranged leaves. Leaves consisting of two parts, leaf-sheath and leaf-blade (cf. *Gramineae,* p. 31). The leaf-sheath forms a tube open only at its junction with the leaf-blade; its lower part is much thickened and in the older (outer) leaves expanded to form a hollow sphere. It is these swollen, concentrically-arranged leaf-sheath bases which form the greater part of the bulb. The upper part of each leaf-sheath is a thinner tube, and these form the neck of the bulb. The leaf-blade is initially solid, approximately hemispherical in cross-section, but becomes hollow and tubular as it matures. The central cavity of the leaf-blade is not continuous with that of the leaf-sheath. The roots are adventitious, arising from the short basal stem. Buds in the axils of some of the lower leaves may develop to form structures

* The tribe *Allieae* is transferred to the family *Amaryllidaceae* in the classification proposed by Hutchinson, on account of its umbellate inflorescence initially enclosed in a spathe. It differs, however, from the typical members of that family in having the ovary superior, in which it agrees with other *Liliaceae.* An alternative view, that of Agardh, it that is should form a separate family, the *Alliaceae.*

similar to the main shoot, still enclosed within the outer leaf-sheaths.

Bulbs are usually harvested when they become dormant at the end of the first year's growth. If they are left in the ground, or replanted in spring, the main stem and those of the axillary buds elongate to produce hollow, swollen, flowering stems, about 1·5m high. These bear no leaves above the bulb, and terminate in a large simple umbel of up to several hundred flowers. The umbel is subtended by a spathe formed of two membranous bracts. The individual flowers are borne on long pedicels; they consist of six free white or lilac perianth segments, about 4 mm long, six stamens of which the three inner have filaments which are very broad and shortly-lobed at the base, and a somewhat triangular ovary with a single slender style.

Cross-pollination is by insects, mainly flies, and the fruit, which usually ripens late in the year, is a loculicidal capsule, with only one or two seeds in each of the three chambers. The seed is black, angular, about 3 mm; the embryo is sharply curved, with a single cylindrical cotyledon and very short radicle. On germination, the radicle emerges and is followed by the greater part of the cotyledon; it is the central part of the cotyledon, bent to form an inverted V, which first comes above ground, while the tip remains in contact with the endosperm in the seed, and acts as a haustorium. Later, the cotyledon straightens, and the first foliage leaf emerges through a slit in the side.

The onion is not known wild, and is perhaps derived from related species in central Asia. It has been cultivated since at least the fourth millenium B.C. for its edible and conveniently storable bulb with high sugar content. The characteristic odour and flavour is due largely to n-propyl disulphide. Grown, often on a field scale, in three main ways in Britain:

(1) *Spring sown for dry bulbs.* The main method; giving bulbs maturing in August or September and storable until the following May. Very numerous cultivars exist, varying in size, shape and colour of skin (outer dry leaf sheaths); usually globular bulbs with straw-coloured to brown skin thick enough to avoid storage damage are preferred. Some cultivars are F.1 hybrids produced by the use of cytoplasmic male sterility. A few cultivars are available as 'onion sets', very small dormant bulbs obtained by late close sowing in previous year and heat treatment to prevent bolting; planted in spring these give a somewhat earlier more easily grown crop.

(2) *Autumn sown for dry bulbs.* Winter hardy cultivars with shorter day-length requirement for bulbing; sown in August to mature in June, to supply the market between the end of the normal storage

period and the harvesting of spring sown bulbs. Cultivars mainly of Japanese origin.

(3) *Salad onions (bunching onions).* Non-bulbing forms in which the green leaves and white bases are eaten fresh; autumn or spring sown, mainly of White Lisbon type.

Allium cepa L. var. ***ascallonicum*** (L.) DC., **shallots**, are a rarely flowering, vegetatively propagated form in which axillary buds develop as bulbs giving a spreading clump of bulbing shoots from a single planted bulb; bulbs used in same way as onions; flavour milder.

Allium fistulosum L., the **Welsh onion,** perhaps derived from *A. altaicum* Pall. of central Asia, is a species with a very slender bulb, occasionally grown and used as salad onions. ***Allium schoenoprasum*** L., **chives**, is a low-growing perennial, widespread as a wild plant in northern Europe, and known in cultivation only since the sixteenth century. Not bulbing, and with purple flowers, stamen filaments all simple; slender cylindrical leaves cut and eaten as flavouring. *A. vineale* L., is a common and sometimes serious weed, wild onion.

Allium porrum L., **leek**, is a long-cultivated tetraploid derivative of the south-west Asian and southern European *A. ampeloprasum* L., of which it is often treated as var. *porrum* (L.) Gay. It has broad flat leaf blades and, in present-day forms, thickened leaf sheaths forming a cylindrical not bulbous edible shoot base. The filaments of the inner stamens are very broad with long lateral teeth exceeding the anthers. Consumed fresh in autumn; some cultivars are winter hardy and can be used in spring.

Allium sativum L., **garlic**, derived from the central Asian *A. longicuspis* Reg., has been cultivated, especially in the Mediterranean area, since the fourth millenium B.C. for its pungent flavour due to diallyl disulphide. Leaves flat, umbels rarely produced and then containing bulbils. Bulbs white, compound and splitting into numerous angular offset bulbs (cloves); vegetatively propagated by cloves planted in autumn or early spring.

Asparagus officinalis L., **asparagus,** belongs to a distinct tribe, with flowers in racemes. It is a rhizomatous perennial, with erect annual stems; it is the tips of these stems which are eaten in the young stage. Fully-developed stems bear only small scale-leaves; photosynthesis carried out by needle-like *cladodes,* stem structures borne in clusters in the axils of the scale-leaves. Dioecious, flowers greenish-white

axillary, single or in pairs; female plants bear red globular berries. Grown as perennial, but propagated by seed, not vegetatively. Male plants outyield female.

Ornamentals

Many members of the family are grown as ornamentals for their conspicuous flowers, used for garden decoration or marketed as cut flowers or pot plants. The genus *Lilium*, the lilies, with very numerous cultivated species and interspecific hybrids, has the bulb scaly, basal or stem rooting. Lilies are propagated by seeds, axillary bulbils or from individual bulb-scales treated as cuttings. *Hyacinthus orientalis* L., the hyacinth, has a long lasting bulb composed of scale leaves and the thickened bases of the foliage leaves. The inflorescence, a leafless raceme of tubular flowers, is terminal and growth of the bulb is continued by the bud in the axil of the innermost foliage leaf. The older lower part of the very short stem dies away; no offset or daughter bulbs are produced, and propagation (other than by seed for the development of new cultivars) is entirely artificial by cutting or scooping of the bulb base to induce the formation of adventitious bulbils. Inflorescence initials are formed after the foliage has died down, normally after the bulbs have been lifted in summer; cool storage of the dry bulbs induces fasciation of the inflorescence, giving a denser flower arrangement.

Tulips, including the composite cultivated group known as *Tulipa gesneriana* L., and crosses of these with other species, have a bulb composed of thick tubular scale leaves only, the broad foliage leaves being borne on the flowering stem, which has usually a single large upright terminal flower. The bulb is short-lived, breaking up each year into a cluster of daughter bulbs formed from buds in axils of the scale leaves. Extensively cultivated in very numerous cultivars for cut flowers and retail bulb sale.

Phormium tenax Forst., New Zealand flax, and species of *Sansevieria*, bowstring hemp, are grown in sub-tropical or warm temperate areas for the fibre obtained from their long stiff linear leaves.

AMARYLLIDACEAE

The *Amaryllidaceae* have flowers basically similar to those of the *Liliaceae*, but the ovary is inferior and there is a spathe-like bract at the base of the flowers.

Narcissus, extensively grown for cut flowers and bulb production, has the perianth segments joined at the base and bearing prominent adaxial outgrowths joined to form the tubular *corona*. A very large

number of cultivars, mainly derived from *Narcissus pseudo-narcissus* L., and related species with yellow perianth and long yellow trumpet-like coronas (daffodils) and crosses of these with *N. poeticus* L., pheasants-eye narcissus, with white perianth and short red-rimmed corona, and other species, are grown, giving a wide range of corona lengths and flower colours. The bulb is similar in structure to that of the hyacinth, with scale leaves and the bases of foliage leaves, but is monopodial, with the inflorescence in the axil of the innermost foliage leaf. The bulb eventually forms a clump by the development of daughter bulbs from buds in the axils of the lower foliage leaves. The flower bud for the following year is produced before the foliage dies down in summer, but its further development, and consequently the time of flowering, is markedly influenced by temperature during the storage period of the dry bulb.

Agave sisalana Perr. (sometimes placed in a separate family *Agavaceae*) is a sub-tropical crop grown for the leaf fibre sisal.

IRIDACEAE

In the *Iridaceae* the flowers are in general similar in structure to those of the *Liliaceae*, but have an inferior ovary and the stamens reduced to three, the anthers dehiscing extrorsely.

In the genus *Iris* the three style branches are petalloid, crested above the outward facing stigmatic surface, the inner perianth segments usually erect (standards) and the outer ones partly reflexed (falls); there are several flowers in each spathe. The species are numerous and vary greatly in growth-habit and size. Commonly grown types include the large hybrid group known as *Iris germanica* L., flag iris, with stout shallow rhizomes and large flowers bearded on the upper surface of the falls; *I. xiphium* L. Spanish iris, and their earlier flowering hybrid derivatives Dutch iris, commonly grown for cut flowers, bulbous with broad round-ended unbearded falls and narrow standards; and *I. xiphioides* Ehr., English iris (although of southern European origin), similar but later flowering with shorter broader standards.

Crocus has narrow leaves and almost sessile flowers with all six perianth segments similar in form. The very short stem forms a corm surrounded by the sheathing but not fleshy bases of the leaves; increase is by production of daughter corms from axillary buds. Numerous species are cultivated, some flowering in autumn, but the majority in early spring. Most commonly grown are the Dutch crocuses, hybrids derived from *C. vernus* Hill and *C. flavus* Weston (*C. aureus* Sm.). *C. sativus* L., saffron, is an autumn flowering species

formerly grown in Britain, the dried stigmas of which provide the spice saffron; some 800 flowers are required to produce 1 g of spice.

Gladiolus has somewhat zygomorphic flowers with unequal perianth segments joined at the base and simple styles; they are borne in dense racemes arising from the large flattened corm, with broad sword-like leaves borne on the lower part of the flowering stem. The corm consists of several internodes and is surrounded by the thin sheathing bases of the lower leaves; it normally dies away each year, being replaced by a new corm formed from the internodes above it. Axillary buds form very small daughter corms (spawn), which are grown on to reach flowering size. The large-flowering gladioli commonly grown in Britain for cut flowers are not winter hardy and are derived from complex crosses of South African species including *Gladiolus* × *gandavensis* Van Houtte, *G. primulinus* Baker and others.

OTHER FAMILIES

The following families may be briefly discussed as including crop plants which are of importance in world agriculture, but which cannot be grown in Britain.

The *Dioscoreaceae,* mainly climbing plants with leaves that are unusual amongst monocotyledons in being broad and net-veined, and with flowers of the general liliaceous type but small and inconspicuous, and usually unisexual, includes *Dioscorea alata* L., yam, widely cultivated in the wet tropics for the edible subterranean tubers. The *Araceae,* with much reduced usually unisexual flowers without perianth borne on a short *spadix* surrounded by a leaf-like *spathe,* includes two species of cocoyam, cultivated for their tubers in the same way as yams, and replacing these in some areas. They are *Colocasia esculenta* (L.) Schott, with peltate leaves, probably of south-eastern Asian origin, known in parts of tropical Africa as old cocoyam, and *Xanthosoma sagittifolia* (L.) Schott, of American origin, known as new cocoyam.

The *Palmaceae* are trees, with solid stems in which the ground tissue is extensively lignified, forming a trunk often covered by the persistent bases of the large usually pinnate leaves. The flowers are usually small in crowded racemes, often unisexual and with two of the three carpels in the female flowers sterile, giving a single-seeded indehiscent fruit. *Cocos nucifera* L., coconut, is widely cultivated in plantations lasting for 20 to 80 years in warm sub-tropical maritime areas. The fruit, which is naturally distributed by floating in the sea, is drupelike in structure, with thin waterproof epicarp, dry fibrous mesocarp (produces coir, used for matting), and stony endocarp

(shell). The single very large seed has a thin testa adherent to the inner surface of the endocarp, massive endosperm with a high oil content and a relatively small embryo (*c.* 2 cm) embedded in the solid outer endosperm; the central non-cellular liquid endosperm is the 'milk'. The ripe coconuts are dehusked, the shell cracked, and the endosperm dried as copra (containing 60% of edible oil melting at 22°C, used in margarine manufacture), or shredded and vacuum dried as desiccated coconut.

Elaeis guineensis Jacq., oil palm, is cultivated in West Africa for its somewhat similar but much smaller drupes borne in large clusters. The fruits differ however in that the mesocarp, as well as the endosperm, consists of oily parenchyma. Only the heterozygous thin endocarp *tenera* forms are cultivated. The mesocarp with 50–65% oil produces palm oil, the endosperm, with 45–50%, palm kernel oil; both are edible and used in margarine manufacture. *Phoenix dactylifera* L., date, bears long racemes of succulent fruit, which is a one-seeded berry, the pericarp with very high sugar content, and the seed (stone) with cellulose as the food reserve of the endosperm. North African; dioecious, and plantations consist of female trees with about 0·3% of males; often artificially pollinated. Very numerous cultivars exist. *Metroxylon sagu* Rottb. and other species, sago palms, are felled and starch extracted from the ground parenchyma of the trunk. Sago consists of dried granules of partially gelatinized starch.

Other tropical monocotyledonous crops, of which the products are imported, include various fruits and spices. Pineapples, *Ananas comosus* (L.) Merr., in the *Bromeliaceae,* are multiple fruits derived from a compact flower spike, in which axis, bracts and floral parts all become succulent, with high sugar and vitamin A and C content. Cultivars are clones, vegetatively multiplied and self-incompatible so that, since plantations consist of one cultivar only, the fruit is seedless. Bananas, *Musa sapientum* L., and other species or hybrids, in the *Musaceae,* are borne on large tree-like herbs with a pseudo-trunk formed of leaf bases through which the flowering stem rises. The fruit is a parthenocarpically produced seedless berry formed from a tricarpellary inferior ovary, the peel being the receptacular tissue and the pulp, with high starch and sugar content, the carpellary tissue.

The family *Zingiberaceae,* with zygomorphic flowers with one stamen only, includes ginger, *Zingiber officinale* Rosc. and turmeric, *Curcuma longa* L.; in both the rhizome is used for flavouring. The *Orchidaceae,* with highly specialized flowers with united style and stamens, includes vanilla, *Vanilla planifolia* Andr., a climbing Central American orchid of which the elongated fruits, formed from the numerous-seeded inferior ovary, are used for flavouring.

3

GRAMINEAE: GENERAL

The *Gramineae,* the grass family, is a large family of world-wide distribution, with some 500 genera and well over 5 000 species. Both floral and vegetative structure are highly specialized, and members of the family are readily recognized; with the exception of the bamboos, which are mainly tropical or sub-tropical and have woody stems, all are herbaceous plants. The majority show the special growth-habit of grasses, making vegetative growth with very little elongation of the stems, so that at this stage most of the aerial part of the plant consists of leaf, the stem and buds being at or near ground-level. It is this habit which makes them ideal grazing plants, since the animals feeding on them eat off only the leaves, and the stem and buds remain undamaged. Grasses form the main food of all grazing animals, and hence are of outstanding importance in any agriculture involving livestock. In addition, the cereals, which are large-seeded annual grasses grown for the food-reserves in the endosperm, are amongst the most important of arable crops. The *Gramineae* is thus unquestionably the most important family of flowering plants from the agricultural point of view.

THE GRASS FLOWER

The grass flower may be regarded as an extremely reduced form of the basic monocotyledonous type, adapted to wind-pollination. In this basic type, as exemplified by the *Liliaceae,* there is a perianth of six segments in two whorls, six stamens also in two whorls, and three united carpels. In the *Gramineae* the perianth is reduced either to a single whorl of three, as in some bamboos, or more commonly to two segments only; these are small scale-like structures known as *lodicules.* Six stamens are found in some grasses, as, for example, in rice, but in the majority only one whorl of three is present. The gynaecium is reduced always to a single-chambered, one-seeded ovary, which bears usually two feathery styles. Such styles with their feathery, stigmatic branches may be considered as an adaptation to

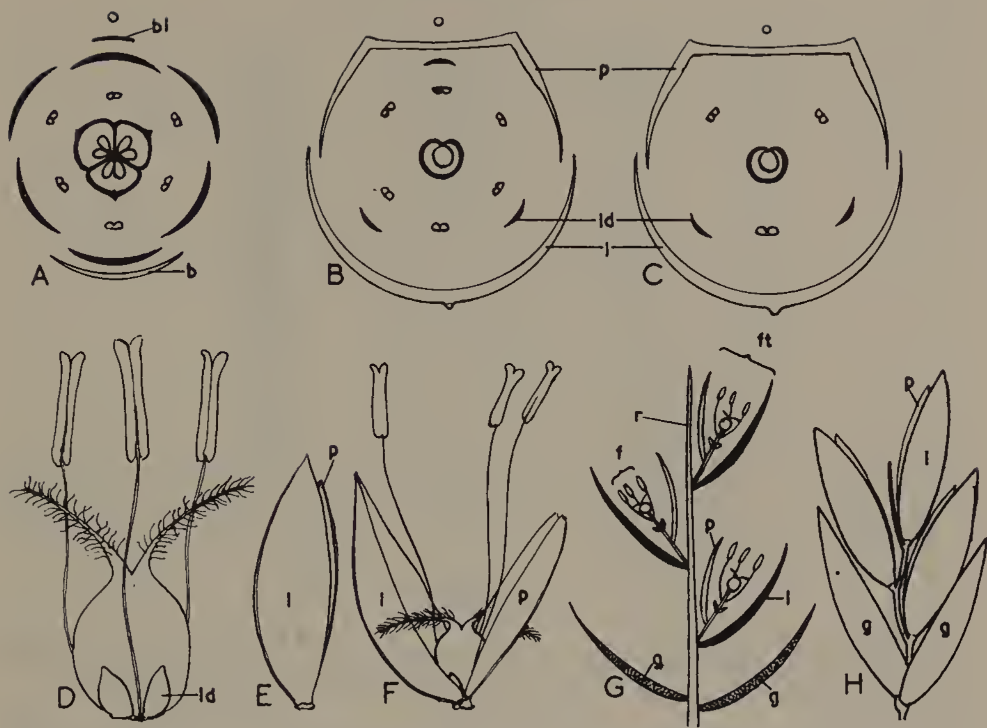


Fig. 3. *Gramineae,* flower and inflorescence. A, floral diagram of *Liliaceae;* B, of bamboo; C, of typical grass. D, grass flower. E, single floret, closed; F, open. G, diagram of structure of typical spikelet. H, spikelet in side view. *b,* bract. *bl,* bracteole. *f,* flower. *ft,* floret. *g,* glume. *l,* lemma. *ld,* lodicule. *p,* palea. *r,* rachilla.

wind-pollination, as providing a large receptive area to catch wind-blown pollen. The stamens also, with their long filaments and large versatile anthers, are adapted to this method of pollination.

The perianth segments, being reduced to small, scale-like lodicules, provide no protection for the developing flower, and the protective function is carried out by bracts. Each flower is subtended by a bract, the *lemma,* and bears on its axis a bracteole, the *palea.* Both lemma and palea are strongly concave on their inner face, and the margins of the lemma usually enclose the edges of the two-keeled palea, so that the true flower is completely surrounded by them. This association of lemma and palea with the true flower (lodicules, stamens and carpel) is so constant that it is usual to speak of the whole structure as a grass *floret.*

Inflorescence

The florets are arranged to form short spikes known as *spikelets.* The axis of the spikelet, on which the sessile florets are borne, is known as the *rachilla*. At its base is a pair of bracts not subtending flowers; these are known as *glumes.* The spikelet then consists of a pair of

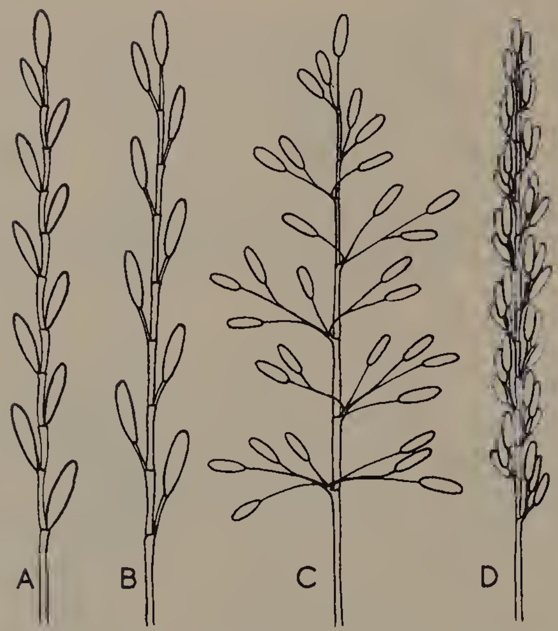


Fig. 4. Diagrams of types of grass inflorescence. A, spike. B, raceme. C, spreading panicle. D, spike-like panicle. Each ellipse represents a complete spikelet.

glumes, and a rachilla bearing a number of florets; the number varies from one to about twenty. This spikelet is the basic unit of the whole inflorescence, which consists always of a series of spikelets. These are arranged to form either a *spike* (strictly a spike of spikelets) where they are sessile on the axis or *rachis*; a compound raceme or *panicle* (strictly a panicle of spikelets) where the spikelets are arranged on a repeatedly branched axis; or occasionally as a simple *raceme* (raceme of spikelets), where the structure is similar to that of a spike, but the spikelets are stalked, not sessile.

Spikes are usually simple, but branched or clustered spikes are found in some grasses (e.g. *Cynodon, Spartina*). The number of spikelets at each node of the spike also varies; there is, for instance, one spikelet per node in wheat, three in barley. Panicles also show considerable variation, particularly in the length of the branches on which the spikelets are borne, and the distance apart of the nodes at which the branches arise. Thus in oats, where the nodes are distant and the branches long, an open or *spreading panicle* is formed; in timothy, where the nodes are closely spaced and the branches short, the spikelets are tightly packed to form a dense cylindrical ear, known as a contracted or *spike-like panicle.*

Pollination. The developing stamens and carpel are completely enclosed within the lemma and palea, and cross-pollination can only take place if these structures separate. In the majority of grasses this

takes place when the anthers are mature; the lodicules become fully turgid, swelling up to force apart the lemma and palea. The filaments of the stamens increase rapidly in length and the anthers come to hang freely outside the lemma and palea, and dehisce, setting free the loose, powdery pollen, which is carried by the wind to other plants. The stigmas are usually exposed later—that is, the flowers are *protandrous.* After pollination has taken place the lodicules shrivel, and the lemma and palea resume their original closed position and remain covering the carpel during the whole development of the fruit. This account of the actual flowering or *anthesis* applies to the majority of grasses, but some exceptions occur. A small number of grasses are *protogynous* (e.g. *Anthoxanthum*); in these there are no lodicules, and the stigma emerges first between the apex of the palea and the lemma, and is followed by the anthers. Occasionally, as in wheat, the anthers dehisce and deposit pollen on the stigma before the floret opens so that self-pollination is the general rule. Such self-pollination of an unopened floret is known as *cleistogamy.* The subsequent opening of the floret is usually too late to be effective, although it may allow a very small and, for most purposes, negligible percentage of cross-pollination to occur.

Caryopsis. If pollination is effective, the single ovule in the carpel is fertilized, and develops to form an endospermic seed. This remains always enclosed within the *pericarp* formed from the carpel wall. The mature pericarp is very thin (except in some bamboos, in which it becomes succulent), and it adheres to the still thinner testa. The special type of indehiscent fruit so formed is known as a *caryopsis.* In the great majority of grasses the caryopsis remains enclosed within the lemma and palea even when mature, and the inflorescence breaks up (*disarticulates*) so that the caryopsis is not set free, but is shed as part of a more or less complicated structure, which may include not only lemma and palea but also glumes. The whole structure is not of course a true seed in the botanical sense, although it is usually referred to agriculturally as a 'seed'; botanically it is most conveniently called a *diaspore* (see p. 26). Only in a rather small number of naturally-occurring grasses, not found in Britain (e.g. *Sporobolus,* the drop-seed grasses), is the caryopsis shed without coverings; in a number of cereals mainly used for human food (e.g. wheat, rye, maize) forms have been selected in which the naked caryopsis threshes out.

A wheat grain may be taken as an example of a caryopsis. It is an ovoid structure, pointed at the lower end, where it was attached to the floret, and blunt at the upper end, where the style branches were

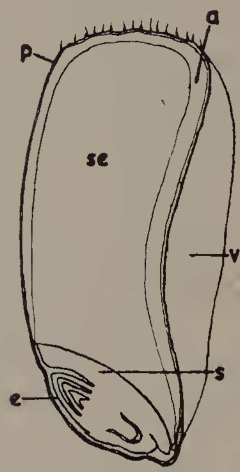


Fig. 5. Diagrammatic vertical section of wheat caryopsis, ×7. *a,* aleurone layer. *e,* embryo. *p,* pericarp and testa. *s,* scutellum. *se,* starch parenchyma of endosperm. *v,* ventral groove.

originally present. It is rounded on the dorsal surface (the surface facing the lemma when the caryopsis was enclosed in the lemma and palea) and marked by a deep groove on the other, ventral side. The whole surface is covered by the fused pericarp and testa, which consist of a few layers only of dead, crushed cells. At the lower end of the dorsal surface the embryo shows up as a small oval area, over which the pericarp and testa are somewhat wrinkled. The remainder of the interior of the caryopsis consists of the endosperm, a mass of polygonal thin-walled cells containing starch grains and some protein. Its outer layer is specialized as the *aleurone layer,* in which the cells are approximately cubical, and contain protein grains. A very thin residue of nucellar tissue (perisperm) may sometimes be seen between the testa and aleurone layer.

The embryo consists of a flattened oval structure, the *scutellum,* in contact with the endosperm, and the cylindrical shoot and root region attached to the scutellum on its outer surface. The shoot region consists of the hollow tubular *coleoptile,* within which is the small conical stem apex, surrounded by two or three rudimentary leaves. The root region consists also of a hollow tubular structure, the *coleorhiza,* which is fused with the scutellum for the greater part of its length, and encloses the short primary root, which shows a well-marked root-cap. Rudimentary lateral roots are present as small projections at the sides of the lower part of the stem region where this joins the scutellum; each of these is covered by a sheath continuous with the coleorhiza.

The morphological interpretation of these structures is not easy, and cannot be fully discussed here. The simplest view is that the

scutellum is the single cotyledon, with the *epiblast,* where this is present, a vestigial remnant of the second cotyledon, and the coleoptile the bladeless first leaf or prophyll (p. 33) of the shoot. An alternative view, based on the comparison of wheat with various other grass embryos, and on the course of the procambial strands which represent the rudimentary vascular system of the embryo, is that scutellum and coleoptile together represent the single cotyledon of the embryo. On this interpretation, the scutellum is regarded as a part of the cotyledon which has become modified as a food-absorbing organ; it may be noted that on germination it secretes enzymes and is responsible for transfer of food material from the endosperm to the other parts of the embryo, but does not itself show any further growth.

Variations in spikelet structure

It has already been mentioned that the spikelet may contain from one to many florets; the various parts of the spikelet may also show very considerable variation.

Glumes. The two glumes present may be equal or unequal in size; they are usually separate, but may be joined as in slender foxtail. They vary in size from the large, thin, multi-nerved glumes of oats, which completely surround and exceed in length the two or three

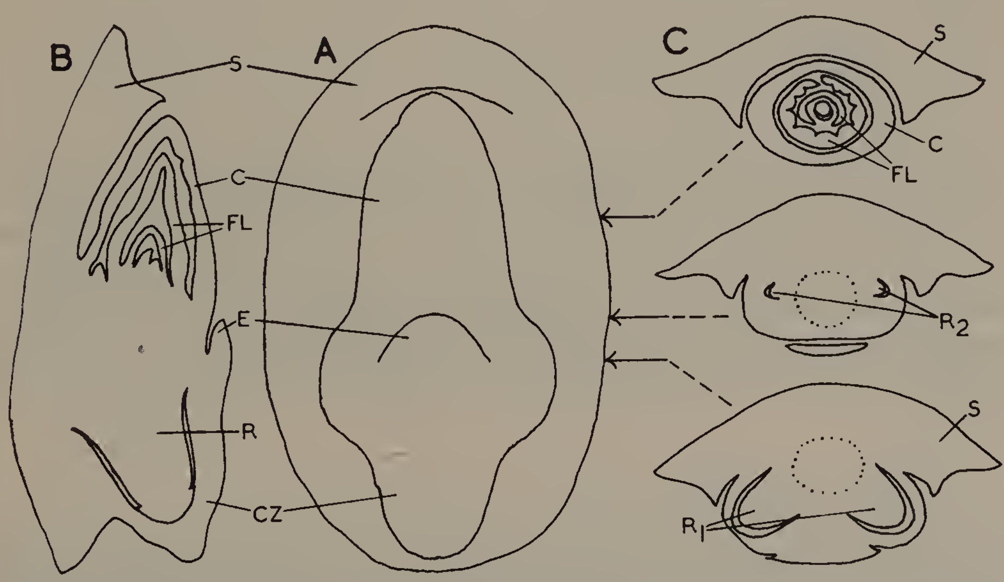


Fig. 6. Wheat embryo. A, in surface view. B, in vertical section. C, transverse sections at three levels, ×20. S, scutellum. C, coleoptile. FL, foliage leaves. E, epiblast. R, radicle. R1, R2, first and second pairs of lateral root initials. CZ, coleorhiza. Adapted from Percival, *The Wheat Plant.*

florets, to minute, almost negligible, scales or facets in mat-grass and rice. They may be stiff and firm as in wheat, or thin and translucent as in tall oat-grass. The apex is often pointed; only rarely, as in timothy and barley, is the point prolonged into an awn-like structure; in *Aegilops* numerous long points are present.

Lemma. The lemma, like the glumes, shows considerable variation in size and texture; it may be round-backed or keeled, awned or awnless. The *awn,* usually a slender, bristle-like outgrowth, may be *terminal* when it arises as a prolongation of the tip of the lemma, *dorsal* when it arises on the back of the lemma, below the tip, or *basal* when its origin is even further down the lemma. It has been shown that large awns such as those of the common varieties of barley, may be responsible for a considerable part of the transpiration of the inflorescence as well as contributing by their photosynthetic activity to the filling of the grains. In addition they may play an effective part in distribution and burying of the seed. This is particularly true of *geniculate awns,* in which the lower part of the awn is spirally twisted and makes a marked angle with the usually finer, straight upper part. The spiral coils and uncoils according to water-content, causing the upper part of the awn to rotate. The shed lemma, enclosing the caryopsis, can be moved about on the surface of the ground by this action, and its sharp lower end tends to enter any cracks present, giving a self-burying effect.

Palea. The palea usually shows little variation; it is typically thin and two-keeled, and is never awned.

Rachilla. The rachilla may be either hairy or glabrous. In a spikelet which breaks up at maturity the rachilla usually disarticulates immediately below the individual florets, so that each separate floret bears a single internode of the rachilla. In one-flowered spikelets the floret may be terminal, as in timothy, in which case no rachilla is present on the floret after separation; or it may be lateral, as in barley, in which case the rachilla is visible standing up from the base of the floret.

The grass diaspore

The diaspore, or 'agricultural seed', that is the structure actually sown, either by natural shedding or after harvesting and threshing, varies according to the structure of the inflorescence and the way in which this breaks up. The true seed of a grass is never seen, since the

caryopsis itself is an indehiscent fruit in which the single seed always remains covered by the pericarp. The main types of structure found are:

(1) Caryopsis only; this is rare and can only occur where the lemma and palea do not wrap closely around the caryopsis. Examples: wheat, rye.

(2) Caryopsis with lemma and palea; the commonest type of 'seed' in grasses. It is found where the rachilla separates above the glumes and, if the spikelet has more than one flower, also between the florets. Examples: rye-grass, cocksfoot, derived from many-flowered spikelets; timothy, bent, from single-flowered spikelets.

In such cases the rachilla (in many-flowered spikelets it is, strictly speaking, only a single internode of the rachilla) forms part of the 'seed' and is visible at the base of the palea. Exceptions to this are those one-flowered spikelets, such as timothy, in which the rachilla is not prolonged beyond the base of the floret. 'Seeds' in which lemma and palea are present will also include the lodicules, but these are not visible without dissection.

(3) Caryopsis with lemma and palea plus one or more male or sterile florets. This is derived usually from a spikelet with only one complete floret. Examples: tall oat-grass (one fertile floret containing caryopsis and one male floret), sweet vernal (one fertile floret containing caryopsis and lemmas only of two sterile florets).

(4) Complete spikelet; this is found where the spikelet separates below the glumes. Examples: slender foxtail (one-flowered spikelet), Yorkshire fog (two-flowered spikelet, of which one floret male only).

(5) Two or more complete spikelets; this is found where the rachis breaks into single-noded sections, each carrying more than one spikelet. Example: wall barley-grass, with three single-flowered spikelets at one node, only the centre one being fertile.

It will be observed that the more valuable species are included in the first two groups, and that the species in the later groups are largely weeds. Increasing complexity of diaspore, while it may make for effective natural distribution and therefore favour the spread of a weed species, makes the cleaning and drilling (and in cereals, grinding) more difficult, and therefore tends to reduce agricultural value.

VEGETATIVE STRUCTURE

The shoot of grasses, like that of other plants, consists of a stem bearing leaves at the nodes. Its appearance, however, may be very different from that of a typical leafy stem, owing to the fact that the lower part of a grass leaf forms a tubular structure, the *leaf-sheath,*

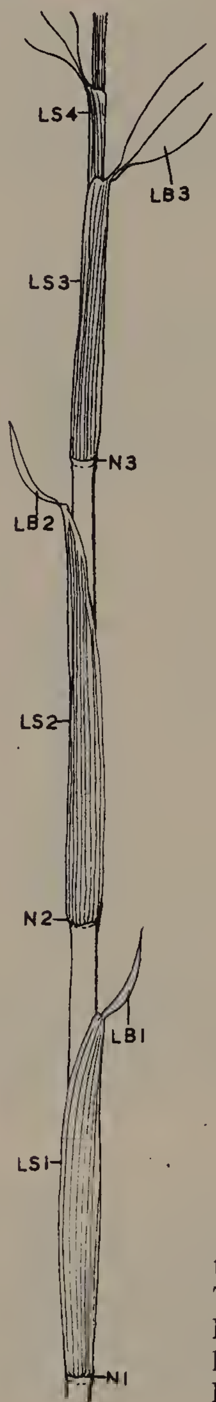


Fig. 7. Diagram of bamboo shoot to show relation of nodes and leaves. The lowest node shown is labelled N1, and the sheath and blade of the leaf arising at this node LS1 and LB1. N2 is the next node above, and so on.

which surrounds and may completely hide the stem. In the majority of common grasses the stem, in the vegetative stage, is extremely short, and the arrangement of the leaves is not readily seen. It is simpler, therefore, to consider first a grass such as bamboo, in which the stem internodes are elongated. A single leaf arises at each node; the leaf arrangement (*phyllotaxy*) is *distichous*—that is, the leaves lie in two opposite ranks. Each leaf arises at a node and its sheath encircles the internode above. The base of the leaf-sheath is attached to the node around the whole circumference of the stem, but the tube so formed is split down one side, and the axillary bud will be found between the sheath and stem on the side opposite to this split. If the leaf-sheath is shorter than the internode above its point of origin, a length of uncovered stem will be visible between the top of the leaf-sheath and the node above. If, however, the leaf-sheath is longer than the next internode, then no stem will be visible, and only by stripping away the next lower leaf will it be possible to see the node at which a leaf originates.

The elongated stem of non-flowering bamboo shoots is exceptional, and the typical vegetative shoot of herbage grasses is one in which the internodes remain very short, so that the apparent axis of the shoot is merely a series of concentric tubular sheaths, with the true stem confined to the base of this. Such a shoot is seen in Fig. 8; a vertical section of the basal part shows that the stem is roughly conical in form, with leaves arising at the closely-crowded nodes. Young

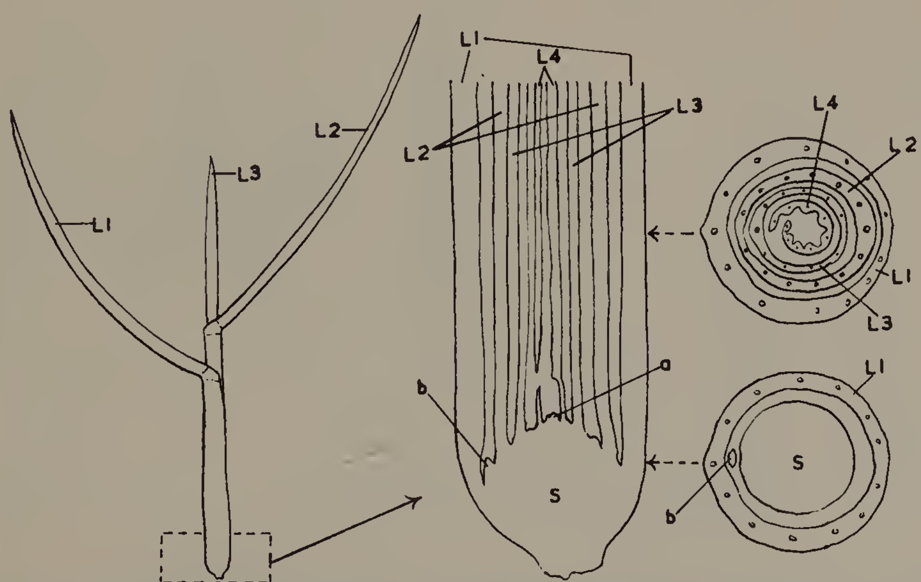


Fig. 8. Single vegetative grass shoot, and diagrammatic longitudinal and transverse sections of its base. L1–4, leaves numbered in succession from oldest to youngest. *a*, stem-apex. *b*, axillary bud. S, stem.

leaves originate as collar-like projections around the apex of the cone and, as they increase in size, grow up through the tube formed by the older leaves.

Axillary buds are formed in the axils of these leaves, and these buds develop to form axillary shoots, each similar in structure to the shoot from which it arises. Usually the axillary shoot so formed grows up between the leaf-sheath of its subtending leaf and that of the next younger leaf, and is first seen when the tips of its leaves emerge above the subtending leaf-sheath. Such a shoot with developing axillary shoots is shown in Fig. 9. Buds in the axils of the leaves of these axillary shoots may in their turn develop to form similar shoots, so that a dense rosette-like tuft of leafy shoots, all with extremely short stems, is gradually built up. This process is particularly conspicuous in cereals, where it is known as *tillering,* and this term is conveniently used as a general name for this type of branching from unelongated stems, the shoots themselves being known as *tillers.*

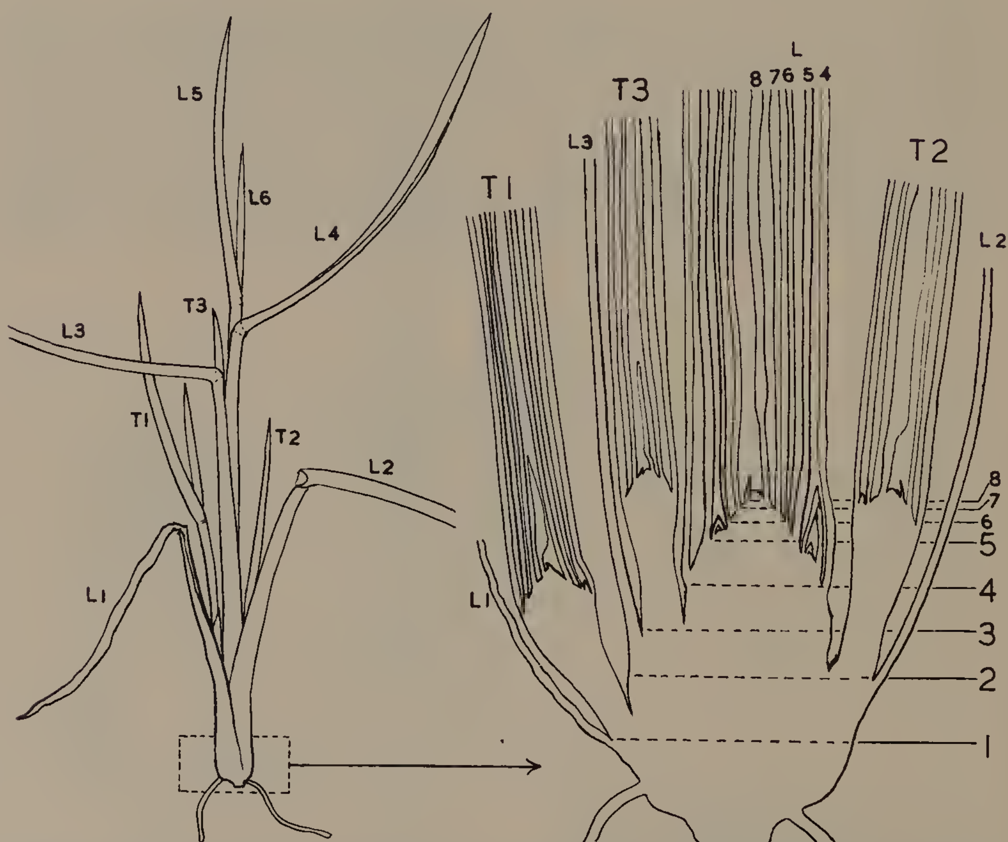


Fig. 9. Shoot after commencement of tillering, and diagrammatic longitudinal section of basal part. L1–8, leaves of main shoot. T1–3, tillers in axils of leaves 1–3. Numbers at right indicate nodes of main shoot.

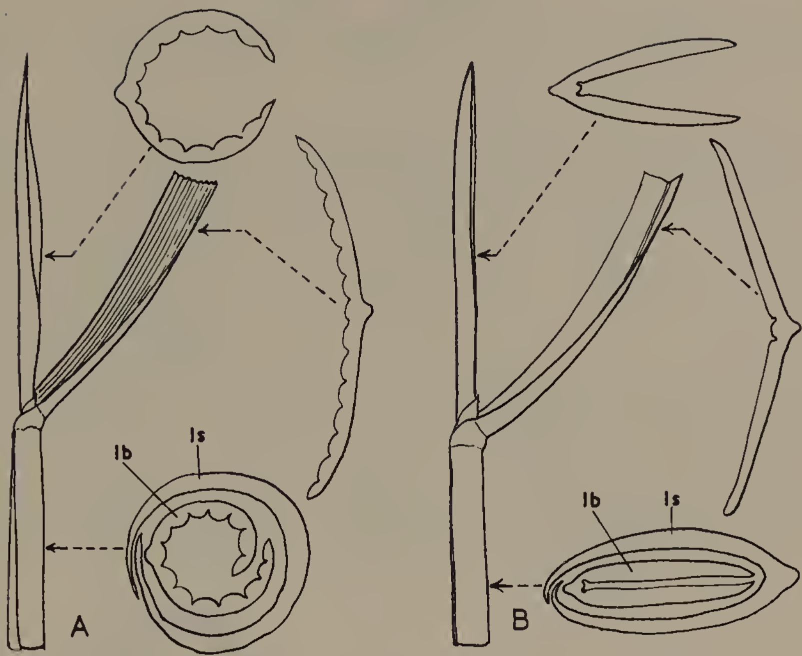


Fig. 10. Diagrams of upper part of vegetative grass shoots, and transverse sections at various levels. A, round shoot, leaf rolled in bud. B, flat shoot, leaf folded in bud. *lb,* leaf-blade. *ls,* leaf-sheath.

Structure of leaf

Each leaf arises as a crescentic projection around the stem-apex; this projection increases rapidly in size and becomes differentiated as an upper part, the leaf-blade, and a lower part, the leaf-sheath; in typical leaves little growth of the sheath takes place until the blade has reached a considerable length, and then the growth of both continues together, the growing zones being at the base of the blade and the base of the sheath. The developing leaf-blade is carried up through the tube formed by the leaf-sheath of the next older leaf, and at this stage is either folded in two or rolled longitudinally. If folded, its outline as seen in transverse section will be a more or less flattened oval; if rolled the section will be round. The shape of the tube formed by the leaf-sheaths conforms to the shape of the young leaf-blades, so that grasses with leaves folded in the young stage have flattened vegetative shoots, while those with rolled leaves have cylindrical shoots. *It should be noted that this distinction applies only to vegetative shoots, flowering shoots in which the stem has elongated are circular in outline whether the leaf-blade is folded or rolled.*

The leaf-sheath may be either *closed* or *open,* that is, may form a complete tube or may be split; this split may extend almost or quite to

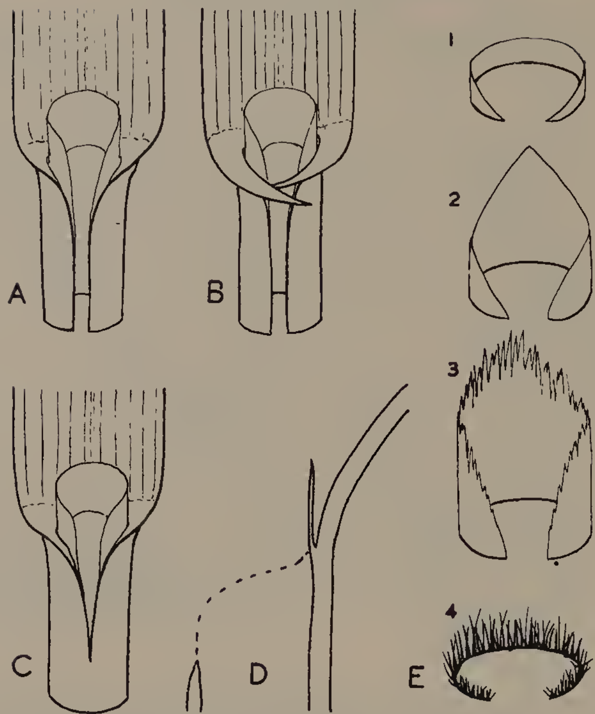


Fig. 11. Junction of leaf sheath and blade. A, auricles absent, sheath open. B, auricles present, sheath open. C, auricles absent, sheath closed. All shown with medium-length blunt ligule. D, diagrammatic vertical section of C. E, ligule types: 1, short, blunt; 2, medium length, acute; 3, long, toothed; 4, represented by ring of hairs.

the base. Frequently the edges of a split sheath overlap. A keel may be present as a projecting ridge down the centre of the sheath.

When the leaf first emerges from the older sheaths surrounding it, the young leaf-blade is erect. As it matures, it gradually approaches the horizontal, making a right angle with the sheath. The junction of blade and sheath is always well-marked, and there is usually a projecting flap, the *ligule,* at this point. This is a thin, erect sheet of non-vascular tissue; it varies in length and shape and is often of value in the identification of grass species in the vegetative stage. The leaf-blade in the majority of grasses flattens out as it matures, and is usually wider than the sheath. At its lower end it may narrow abruptly to the sheath, or its lower corners may be extended as a pair of claw-like projections, the *auricles.*

The mature blade of a typical leaf is always long in proportion to its width, and usually considerably longer than the sheath. It may be *tapering,* with the margins straight and the width greatest at the base, *parallel,* with the margins straight except at the tip, where the blade narrows abruptly to a blunt point, or *broadest near the middle* and tapering to the tip and base. In some grasses the leaves are *bristle-like*

(needle-like, acicular), remaining permanently folded so that the blade forms a more or less solid 'bristle', usually narrower than the sheath.

The upper surface of the leaf-blade may be flat or ribbed; the lower surface is usually flat, but may show a central keel. Both sheath and blade may be glabrous or hairy. The leaf-blade is usually a darker green than the sheath; the lower part of the sheath, not exposed to light, is often white, but may show other colours, e.g. red in the ryegrasses and fescues, yellow in dog's-tail. Such differences are frequently of value in the identification of grasses when not in flower.

The first leaf of a tiller is usually distinctly different from the later leaves; it consists of a two-keeled sheath without blade, and is known as a *prophyll*. Short, bladeless scale-leaves occur on underground stems, and transitional leaves, intermediate between those and typical foliage leaves, may also be found.

Leaf anatomy

The venation of grass leaves is parallel; that is, a number of vascular bundles enter the leaf at the node and extend throughout its length without branching. These veins are surrounded by loosely-arranged

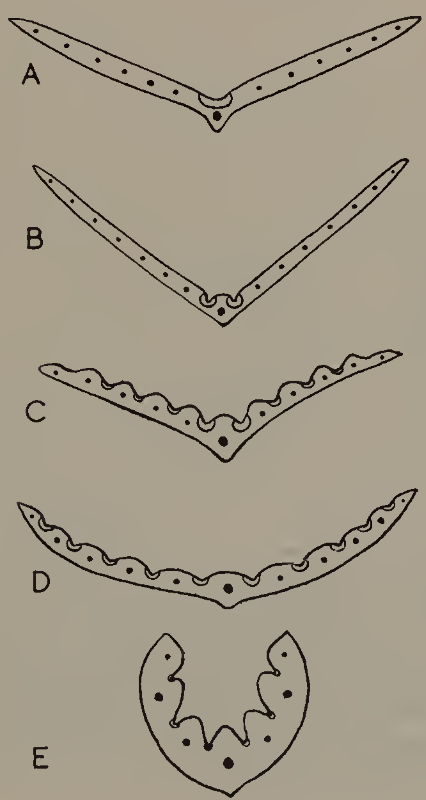


Fig. 12. Diagrammatic transverse sections of leaf-blades of different types. A, folded, upper surface plane, one line of motor-tissue (cocksfoot). B, as A, but two lines motor-tissue (meadow-grass). C, folded, upper surface ribbed (dogstail). D, rolled (timothy). E, bristle-like (small fescue). Motor-tissue outlined, vascular bundles solid black.

chlorophyll-containing parenchyma, the mesophyll, which in turn is covered by the epidermis. This forms a continuous 'skin' over the leaf, the only apertures in it being the stomata, the apertures between the specialized guard-cells. The stomata, through which the bulk of the exchange of gases and water-vapour between the intercellular spaces and the external atmosphere takes place, are present on both surfaces of the leaf-blade of many grasses. In the more xerophytic species, however, they are found only on the upper (adaxial) surface, so that if the leaf-blade is rolled up, either permanently as in the bristle-leaved grasses, or temporarily in response to dry conditions, they all open in to the more or less enclosed space within the tube formed by the rolled blade.

Folding and rolling of the leaf-blade is facilitated by the presence of lines of motor-tissue, consisting of greatly enlarged thin-walled cells of the upper epidermis known as bulliform cells. In folded leaves, a single line of motor-tissue in the centre of the blade (e.g. cocksfoot) or two closely-spaced lines, one on each side of the centre vein (e.g. meadow grasses), act as a hinge, allowing the two halves of the blade to close together. In leaves which roll up, a number of lines of

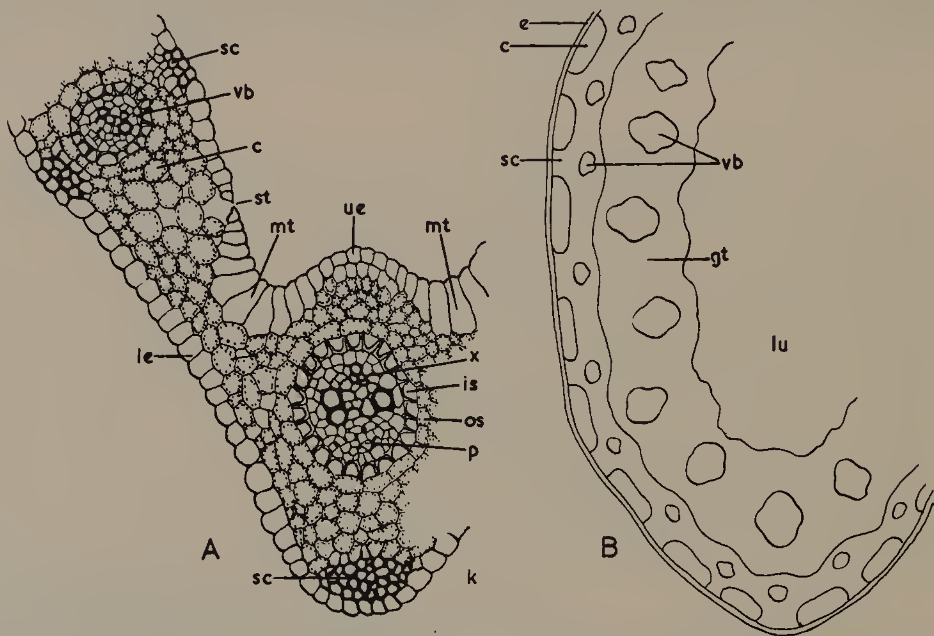


Fig. 13. A, transverse section of part of leaf-blade of smooth-stalked meadow-grass to show arrangement of cells. B, diagram of part of a transverse section of almost mature flowering stem of cocksfoot, to show arrangement of tissues. *vb*, vascular bundle. *x*, xylem, *p*, phloem. *is*, *os*, inner and outer bundle sheaths. *sc*, sclerenchyma. *le*, *ue*, lower and upper epidermis of leaf. *mt*, motor-tissue. *st*, stoma. *c*, chlorenchyma. *e*, epidermis. *gt*, parenchymatous ground-tissue. *lu*, lumen, space formed by breakdown of central ground-tissue of stem. *k*, keel.

motor-tissue are present. When, as is frequently the case, the upper surface of the blade is ribbed, these lines of motor-tissue lie in the grooves between the ribs, and contraction of the cells results in the upper surface becoming strongly concave. Motor-tissue is absent or poorly developed in permanently-folded, bristle-like leaves.

Each vein consists of a single vascular bundle with xylem and phloem surrounded by a bundle-sheath of two layers of cells. In the majority of temperate-region grasses the outer layer is poorly-developed, the inner conspicuous with lignified walls; in such grasses the area between the veins is occupied by rather small uniformly arranged chlorenchyma cells of the mesophyll, and the leaf anatomy is referred to as festucoid. In the *Paniceae* and related tropical grasses the bundle-sheath is a single layer of specialized chlorenchyma, and large mesophyll cells radiate from each vein, with a line of colourless parenchyma cells in the centre of each interveinal space; this is the panicoid type of leaf anatomy (p. 40).

Additional mechanical strength is provided by sclerenchyma associated with the veins. The amount of sclerenchyma present has a marked effect on the palatability of the leaf, and is discussed further on p. 135. Special siliceous cells, with a high silica content, and varying in shape in the different tribes, are present in the epidermis.

Stem anatomy

In the relatively small number of grasses with a solid stem, of which maize may be taken as an example, the stem structure is that of a typical monocotyledon, with scattered bundles embedded in a ground tissue of parenchyma. Each vascular bundle consists of relatively small strands of xylem and phloem, surrounded by a bundle sheath; no cambium is present. In the majority of grasses, however, the vascular bundles are confined to the outer part of the stem, and the central part of the ground tissue breaks down, so that the mature stem is hollow (except at the somewhat swollen nodes, where a solid septum separates the cavities of adjacent internodes). The bundles, being thus confined to the relatively narrow region left, appear less scattered than in maize, and tend to be arranged in two rings as seen in transverse section. The bundles of the inner ring are usually larger; the ground tissue surrounding the bundles of the outer ring becomes thick-walled and lignified, so that these bundles are embedded, in the mature stem, in a ring of sclerenchyma. This schlerenchyma ring has, spaced at intervals around it, projections which extent out to the epidermis, and divide the chlorenchyma, which forms the outer ground tissue, into a series of narrow, vertical strips. The stomata

open into the intercellular spaces of these strips, which remain green and carry on photosynthesis until the final ripening of the fruit and death of the stem. Creeping stems show a somewhat similar structure, but are more often solid. In rhizomes, which grow underground, no chlorophyll is present.

LIFE HISTORY

Germination. Germination is essentially the growth of the root and shoot regions of the embryo at the expense of the food reserves contained in the endosperm. Wheat may be taken as an example in which the grain is large and consists of the caryopsis without any other parts of the spikelet, and in which the progress of germination is therefore readily followed. The grain absorbs water, and the cells of the embryo, living but up to this time dormant, become active. Enzymes present in the aleurone layer and scutellum break down the starch and protein contained in the endosperm cells, and the soluble products are absorbed by the enlarged outer epithelial cells of the scutellum, and pass to the other parts of the embryo. Cell division recommences, and the first slight increase in size of the coleoptile and coleorhiza results in the rupture of the combined pericarp and testa covering them. The coleorhiza increases only slightly in length, and the primary root breaks through it and elongates; the lower pair of lateral roots also break through their sheaths, followed usually by the upper pair. Rather later a fifth lateral root may appear. Meanwhile, the coleoptile elongates and its upper part comes above ground as a tubular structure which surrounds and encloses the remainder of the shoot. Increase in length of the first foliage leaf (the next leaf after the coleoptile) results in this growing up through the tubular coleoptile and emerging through the slit at the top. Successive leaves develop from the short, conical stem-apex to give a shoot-structure similar to that described (p. 29) for a typical vegetative tiller. This may occur without any marked elongation of the stem, but if the grain has been rather deeply drilled, the lower one or two internodes above the coleoptile node may elongate to form the so-called rhizome. This has the effect of bringing the remaining unelongated part of the stem, from the nodes of which tillering will take place, into position just below the soil surface.

Meanwhile the primary and lateral roots have increased further in length and become branched, forming the *seminal root system,* which may persist throughout the life of the plant, but is soon supplemented by adventitious roots developed from the nodes above, and it is these which form the main bulk of the root system of the mature plant.

Tillering. As the main shoot increases in size and number of leaves, tillering begins. This, as has been explained (p. 30), is the development of the buds in the axils of the leaves to form shoots, the internodes of which, like those of the stem from which they arise, remain very short. Secondary tillers arise in the axils of the leaves of these primary tillers, so that a cluster of leafy shoots is developed. As each tiller enlarges, adventitious roots arise from its lower nodes, so that the size of the root system keeps pace with that of the aerial parts. The actual amount of tillering which takes place is very much dependent on conditions, and is discussed further in Chapter 4.

Flower initation. Each tiller during the period of vegetative growth has a conical stem-apex, from which new leaves continually develop. At a certain stage, however, the stem-apex changes from this vegetative condition and produces instead a rudimentary inflorescence. After this change no more leaves are produced by the tiller, and the last one formed is the 'flag' leaf. The change from the vegetative to the flowering condition is primarily a response to day-length, but previous exposure to low temperatures is necessary in some cases.

Stem elongation. Once the change from the vegetative to the flowering condition has taken place in a particular tiller, its further development consists in the increase in size of the structures already present. The remaining immature leaves develop successively to their full size, and at the same time the internodes elongate, carrying the nodes bearing the younger leaves up through the tube formed by the older leaf-sheaths. Elongation of the lower internodes takes place first (the actual growing region being at the base of each internode); each internode starts its growth before that of the one below has ceased, so that normally two or three internodes are elongating at the same time. The final length reached by each internode usually increases progressively up the stem; it is always less than that of the corresponding leaf-sheath, except for the final and longest internode immediately below the inflorescence. This carries the inflorescence, which meanwhile has been increasing in size and complexity, and by now is almost mature, up through the leaf-sheath of the final or flag leaf, a process sometimes known as the 'shooting of the ear'. It usually continues growth until there is a considerable length of bare stem (neck) between the top of the flag leaf sheath and the base of the ear.

Fruiting and death of the tiller. Pollination and fertilization take place, and the caryopsis matures; during the latter process food materials are absorbed from the fertile tiller, and the whole of this

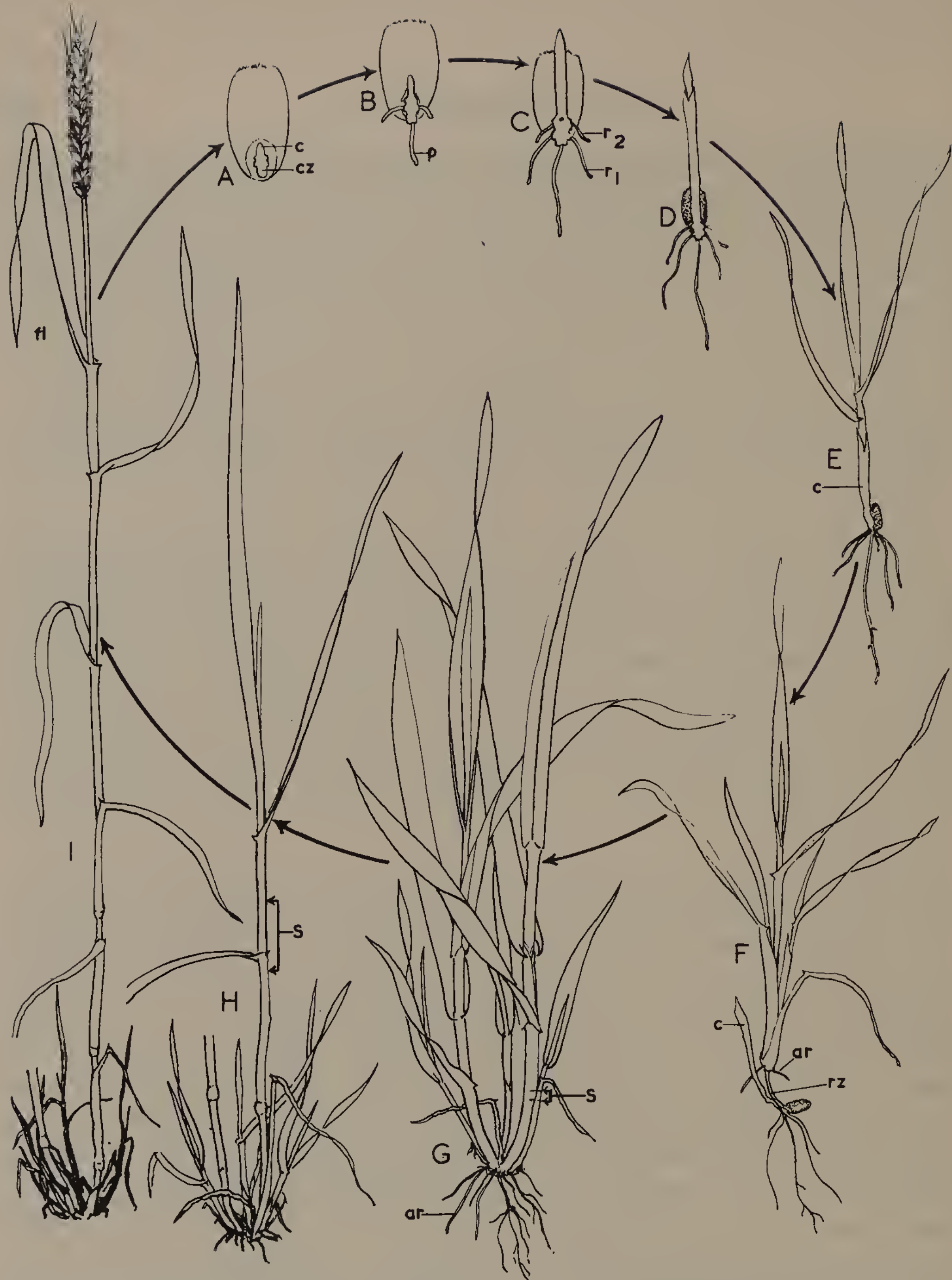


Fig. 14. Life cyle of wheat. A–D, germination. E, young plant before tillering. F, beginning of tillering; elongation of internode above coleoptile to form rhizome has brought tillering nodes near to ground-level, and development of adventitious roots from those nodes has begun. G, further tillering has taken place, and the stem-apex of the larger tillers has changed from the vegetative to the flowering state and elongation of their stems has started. H, tillering has ceased, lower internodes of fertile tillers have elongated, inflorescence well developed, but not yet emerged. I, ear of few fertile tillers emerged, later-formed tillers dying; after this stage pollination and fertilization lead to the development of the mature grain, followed by the death of the plant. (H and I one fertile tiller shown in full; roots largely omitted.) *c*, coleoptile. *cz*, coleorhiza. *p*, primary root. r_1, r_2, first and second pairs of seminal roots. *ar*, adventitious roots from lower nodes of shoots. *rz*, rhizome. *s*, position of spike.

tiller is dead by the time the grains are fully mature. In wheat and other annual grasses all tillers die in this way; in perennial grasses (see p. 132) vegetative tillers are also present, and these remain alive, only the fertile tillers dying.

CLASSIFICATION OF THE GRAMINEAE

The *Gramineae* is a very large family showing a wide range of structure, and since a large number of different members of the family are of agricultural importance, and need to be considered here, either as cereals or as herbage grasses, it is convenient to split it into a number of groups. The largest groups within the family are known as *subfamilies,* and these in turn are split into *tribes*; members of one tribe have a good many characters in common, and a knowledge of the characters of the different tribes provides therefore a useful framework for the knowledge of the individual grasses.

The older classification of the family was based purely on the structure of the inflorescence and spikelet; more recently a large number of morphological and physiological characters have been

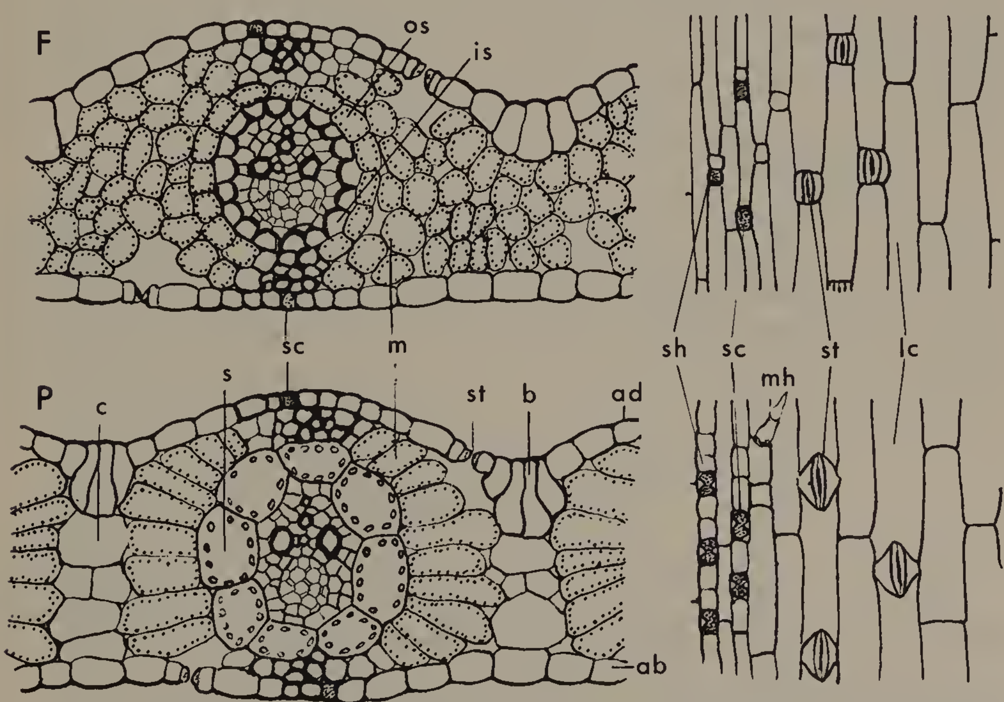


Fig. 15. Diagrams of part of leaf blade in transverse section and abaxial surface view, × *c*. 150. F, leaf of festucoid type; P, of panicoid type. *ab,* abaxial epidermis; *ad,* adaxial epidermis; *b,* bulliform cells; *c,* colourless cells; *is,* inner bundle sheath; *lc,* long cells; *m,* mesophyll; *mh,* micro-hair; *os,* outer bundle sheath; *s,* single bundle sheath; *sc,* silica cell; *sh,* short cells; *st,* stoma.

taken into account as well, in order to produce a more natural classification. There have therefore been some changes in the grouping of grass genera into tribes and of these into sub-families, and some differences of opinion still exist. Two large and important sub-families can be distinguished:

Festucoideae. Mainly temperate-climate tribes, with first foliage leaf narrow, the vascular bundles of the leaf-blades with double bundle sheath, the mesophyll cells uniformly arranged, and the leaf epidermis without micro-hairs and with oblong silica-cells. Stem internodes hollow; spikelets with one to many florets, which may all be fertile, usually disarticulating above the glumes. Embryo relatively small; chromosomes typically large, with basic number usually seven. Photosynthesis follows the usual metabolic pathway via three-carbon-atom compounds.

Panicoideae. Mainly tropical tribes, with first foliage leaf broad. Vascular bundles of leaf-blades with single sheath of large parenchymatous cells with specialized chloroplasts, mesophyll cells often radially arranged, leaf epidermis with two-celled micro-hairs and dumb-bell-shaped silica-cells. Stems often solid; spikelets with two florets, the lower sterile, usually disarticulating below the glumes. Embryo relatively large; chromosomes typically small, with basic number 9 or 10. Often with high photosynthetic capacity via four-carbon-atom compounds.

There are in addition a number of tribes which do not fall clearly into either of these two sub-families, having some of the characters of each. These are variously placed by different authorities in a number of other sub-families, but since few representatives of them are discussed in this book, it is convenient to group them here merely as 'intermediate tribes'.

Tribes of *Gramineae*

	For genera see pages:
Festucoideae (for sub-family characters see above)	
Festuceae. Inflorescence a panicle (except *Lolium*), spikelets many-flowered, glumes short. Starch grains compound, ovary glabrous.	141–66
Brachypodieae. Inflorescence as *Festuceae* or simple raceme. Spikelets as *Festuceae.* Starch grains	

simple, ovary with hairy lobes. (Sometimes included in *Festuceae*.)	166–9
Hordeae. Inflorescence a spike, spikelets one- to many-flowered. Starch grains simple, ovary hairy.	59–96, 170–2
Aveneae. Panicle, spikelets few-flowered, glumes large, awn dorsal, often geniculate. Starch grains compound.	97–110 172–82
Phalarideae. As *Aveneae*, but one floret only complete, others reduced to lemmas. Chromosome number varies. (Sometimes included in *Aveneae*.)	182–4
Agrostideae. Panicle, spikelets one-flowered, glumes larger than floret, awn dorsal. Starch grains compound (Sometimes included in *Aveneae*.)	184–92
Glycerieae. Inflorescence and spikelets as *Festuceae*. Silica-cells few. Starch grains compound. Chromosomes small, basic number 10.	192–3
Nardeae. Spike, spikelets one-flowered, glumes minute. Some panicoid features in leaf epidermis. Starch grains compound. Chromosome basic number 13.	193–4

'Intermediate tribes' (tribes belonging to other sub-families)

Danthonieae. Panicle, spikelets few flowered. Leaf anatomy varied, panicoid or festucoid; starch grains compound; chromosomes small, basic number 6.	194–6
Arundineae. Reed-like plants usually with stout rhizomes. Panicle, spikelets with varied floret number. Starch grains compound. Chromosomes small, basic number 12.	196
Chlorideae. Inflorescence a branched spike of usually one-flowered spikelets. Leaf anatomy often strongly panicoid. Starch grains compound. Chromosomes small, basic number 9 or 10; four-carbon-atom metabolic pathway.	114, 196–7
Oryzeae. Panicle, spikelets with single fertile floret, two lower florets reduced to scales; palea often 3-nerved. Leaf anatomy with some panicoid and special features. Starch grains	

compound. Chromosomes small, basic number 12. 110–14

Bambuseae. A very distinct tribe, with woody stems up to 40 m high, leaf-blades broad with petiole-like construction at base. Flowering infrequent, panicle or a series of pseudo-spikelets with basal bracts. Spikelets several-flowered, lodicules 3, stamens often 6, fruit varied, sometimes succulent. Leaf anatomy with special features. Chromosomes 12. 197

Panicoideae (for sub-family characters see above)

Paniceae. Panicle, spikelets with two florets, the upper fertile, hermaphrodite. Lemma of fertile floret often hard, glumes soft. Starch grains simple. 114–16, 197

Andropogoneae. As *Paniceae,* but spikelets in pairs, one sessile, usually hermaphrodite, the other stalked, sometimes sterile. Lemma and palea soft, often reduced or absent, glumes hard. 116–18, 198

Maydeae. As *Andropogoneae*, but separate male and female spikelets or inflorescences. (Sometimes included in *Andropogoneae.*) 118–27

Cereals and herbage grasses. Certain members of several of these tribes are large-fruited grasses grown for their seed-reserves, that is, cereals; for convenience of treatment these are considered separately in Chapter 5. Wheat, rye and barley belong to the *Hordeae*, oats to the *Aveneae*; these cereals are considered in some detail, and a brief description is given of the mainly tropical or sub-tropical cereals rice (*Oryzeae*), millet (*Paniceae*), sorghum (*Andropogoneae*) and maize (*Maydeae*).

The herbage grasses of importance in Britain all belong to tribes included in the sub-family *Festucoideae*, and these are treated in detail in Chapter 7, together with a brief reference to grasses belonging to other tribes.

4

CEREALS: GENERAL

THE ORIGIN OF CEREALS

The cereals are grasses grown for their large seed reserves. They are derived from large-seeded wild ancestors, and for wild plants large seeds confer an advantage in conditions where annual plants compete strongly for establishment. Today, wild wheats and wild barley are found in some upland areas near the eastern end of the Mediterranean where such conditions prevail. A very dry summer prevents the growth of all perennial vegetation other than rather widely spaced trees. A fair winter rainfall of some 250 mm or more allows vigorous growth of those annuals which by virtue of their large seed reserves and consequent rapidly growing large seedlings are able to compete successfully in the race for establishment when rain allows germination of seeds present in the soil. Not only do the wild cereals have large seed reserves, but their seeds form part of an efficient self-burying diaspore. They thus escape being eaten by rodents or other animals during the summer, and are suitably placed to germinate as soon as sufficient moisture is available. In wild wheat and barley the inflorescence is a spike, and the rachis disarticulates as soon as the grain is ripe, giving single sharp pointed lengths, each with one fertile spikelet attached and arranged so that the lemmas and other structures surrounding the caryopsis, and the awn and hairs which they bear, act as barbs. Thus if the pointed base of the diaspore penetrates into a crevice in the soil, withdrawal is prevented, and in loose soil many of the diaspores reach a satisfactory depth.

In this region, as for example in parts of the Jordan valley, there are found, in areas protected from grazing by domesticated animals, present-day stands of wild wheat and barley estimated to yield 600 kg of grain per hectare. Presumably such stands existed in prehistoric times, and may well have been more extensive then; at a time when all man's food had to be obtained by gathering wild plants and hunting wild animals this wild grain must have been a quite exceptionally good source of food. A yield of 600 kg/ha may seem very low by present-day standards, but in fact it compares favourably with yields of cultivated cereals in Britain during the Middle Ages, and is extra-

ordinarily high for wild plants. Archaeological evidence indicates that mesolithic peoples of this region, known (from the Wadi el Natuf, where their remains were first found) as Natufians, were exploiting these wild cereals between ten and eleven thousand years ago, and mortars, grinding stones, and flint sickle blades have been excavated.

The wild cereal inflorescences disarticulate very rapidly, and can only be harvested during the period of less than a week when they are ripe enough to use but have not yet shattered. There is, however, as one goes up the hillsides, a spread of some three weeks in ripening time, so that a total harvesting time of nearly four weeks was available. Present-day trials on similar wild wheat stands in Turkey, using the ancient type of flint-edged sickle, have shown that a man can harvest one kilogram of clean grain an hour; a mesolithic family, working all the hours of daylight, could thus harvest a very substantial fraction of their annual food requirement during the time available.

The edible caryopsis of the wild cereals is firmly held within the lemmas and other parts of the diaspore and cannot be separated by threshing. Laborious grinding off of the inedible chaff would be necessary, and since the food reserves in the endosperm are mainly starch, largely indigestible raw, some form of cooking would be required; that these problems were solved is witnessed by the grinding stones and the eventual development of querns and bread ovens.

For the peoples in the immediate neighbourhood of the wild cereals there would be initially no incentive to develop any techniques other than the exploitation of the natural stands. Others, nomadic or settled farther away, and perhaps making incursions to harvest the grain, or loot that already harvested, must have found that grains accidently trodden into the ground would grow and in turn produce a harvest in new areas. The intentional sowing and harvesting in these new localities would be the beginnings of agriculture. This would thus have started in the areas fringing the natural habitats of the wild cereals; alternatively it has been suggested that the domestication of animals, which occurred at very roughly the same time, may have resulted in such grazing pressure on the natural stands that intentional cultivation became necessary in the primary cereal areas.

In any event, the cultivation of wheat and barley developed and extended. Conscious selection of improved forms is perhaps unlikely, but the change from wild to cultivated conditions would automatically alter the selection pressures acting on the plants. Extreme fragility of the rachis, resulting in very rapid shattering, would tend to disappear since diaspores from plants with this character would be likely to have been shed before harvest took place, and therefore be

lost. The self-burying habit would no longer be of value, and less hairy and less barbed forms would be preserved. Forms with long seed dormancy, valuable in the wild populations as ensuring survival in a year when the breaking of the drought was only temporary, would be eliminated, since they would not have ripened by the time the cultivated crop was harvested. Thus cultivation allowed the accumulation of mutations which changed the cereals from wild types to ones more useful to man; archaeological evidence from sites where recognizable carbonized grains have been excavated shows that by the seventh millenium B.C. both wheat and barley of types clearly identifiable as cultivated were wide-spread in the hilly regions of south-western Asia. By the fifth millenium cultivation had extended to the river valleys of Iraq and Egypt, where conditions were very different from those of the original habitat. The assured food supply provided by agriculture allowed the establishment of permanent settlements and the transition to the more advanced neolithic culture, which spread relatively rapidly through south-western Asia, North Africa and Europe, so that by some time in the fourth millenium agriculture reached Britain.

Considerable diversification of the cereals took place; at a quite early date naked forms of barley, in which the caryopsis threshed out cleanly, became available, and rather later wheats with this character were used. Where the cereal is used as human food such naked forms have of course a great advantage, and they have therefore to a large extent replaced the hulled forms. Where cereals are used for brewing—a use discovered at a very early stage—or for feeding to animals—which became necessary when domesticated animals were employed as the motive power for ploughs and wheeled vehicles, and hence needed concentrated food—the hulled forms may be more satisfactory, and they have therefore been retained for these purposes.

The wild ancestors of oats and rye also occur in south-western Asia, but there is no evidence that they were ever cultivated there. They do however spread into cultivated wheat and barley crops as weeds. It must be recognized that primitive agricultural methods necessarily result in weedy crops, and that since seed-cleaning would be confined to very simple winnowing, all seed corn would be heavily contaminated with weed seeds. Thus what apparently happened was that, as this weedy seed corn was carried northwards by neolithic migrations or 'trade', the areas in which it was cultivated became progressively less favourable for the wheat or barley, and more favourable for the oats or rye, which are more tolerant of colder and damper conditions. Eventually the original crops species disappeared and in central and

northern Europe, by about the first millenium B.C., oats and rye, having by then lost their wild characters in the same way that wheat and barley had earlier, were being cultivated as crops in their own right.

This spread of cereals from their original arid habitat to the much more humid climate of northern and western Europe involved problems of storage. In south-western Asia the grain as harvested would have a very low water content; the chaff would be brittle enough to mill off readily, and the caryopsis dry enough to store safely. Farther north this would not be true, and remains of structures interpreted as drying ovens suggest that artificial drying was the general practice. Harvesting was apparently of the ears only, these being dried and probably threshed immediately, the parched grain being stored in silo pits which soon became contaminated with fungi and needed frequent replacement. Seed corn would need to be treated differently, and small above-ground granaries have been postulated. At some later date in early historic times it must have come to be appreciated that, except in very wet years, corn cut with long straw could safely be stacked in sheaf, the straw gradually absorbing excess moisture from the grain. This technique, with later threshing from the rick, lasted throughout historic times, and it was not until the introduction of the combine harvester that the problem of artificial grain drying had once again to be faced.

There is thus good evidence that the cereals (other than maize) now commonly cultivated in Britain and the rest of Europe originated in south-western Asia and adjacent areas, where alone their wild ancestors are indigenous. Their cultivation there appears to have been the beginning of agriculture, and the assured food supply which resulted from the cultivation of crops and the domestication of animals released man from the onerous and ever-present tasks of food gathering and hunting and allowed his advancement in other directions. This led to the development of pottery, and later to the use of metals and eventually to something that can be called civilization. In general it was in the areas adjacent to the habitat of the wild cereals that these developments first occurred, and from there spread out in all directions.

This outline of the source of our common cereals and of European agriculture does not imply that this was the sole origin; it is highly probable that agriculture was developed independently in many different parts of the world, and at different times. In some cases legumes may have been the first crops, rather than cereals. The cultivation of tropical cereals, such as rice in south eastern Asia, was very likely developed independently. Certainly maize cultivation was

developed in America at a time when there is no evidence for any possible link with Old World cereal growing. Some of the millets were cultivated in Europe during the neolithic period but were later abandoned, and there is no clear evidence of their origin. Sorghum is apparently African, but again evidence of the time and place of early cultivation is lacking. It is to be expected that further archaeological exploration will cast more light on the origin and migration of all the cereals. For the present large areas of uncertainty remain, and the picture outlined here may need to be modified; there are for example unexplained reports of grinding stones and flint sickle teeth dated to the thirteenth millenium B.C. in Nubia, where no known wild cereal exists, and even of barley, apparently cultivated, then or earlier.

The present-day representatives of all the cereal species are separated from their early cultivated ancestors by some thousands of years of selection by climatic and agronomic factors and by human choice. For most of this time corn fields would be mixed populations of a wide range of forms, mutations would occur and be accumulated or eliminated, chance crosses would take place and their offspring segregate; where special local conditions existed local land-races and specialized local populations would develop. Conscious selection would play a part, at first by farmers, later, and increasingly during the past two hundred years, by plant breeders. For the most part selection has been in the direction of higher and more regular yield, both of total produce and of usable caryopsis, of higher quality for the purpose for which the grain was used, and of the elimination of inconvenient types of diaspore and of unwanted hairy and dark-coloured forms. With the development of higher standards of agriculture, the increased use of fertilizers and the progress of mechanization, the pace of change has quickened. The grower's and consumer's changing demands and the greatly increased resources of the scientific plant breeder combine to make present-day cereal species a constantly changing series of cultivars, each replaced after a few years by new and improved forms. This makes for increasing efficiency and increasing output of food, but, taking place almost everywhere, it has the unfortunate side effect of diminishing the world-wide diversity of forms and impoverishing the available range of potentially useful genes, which are the plant breeder's raw material for future work. This can be partially offset by the maintenance of collections of obsolescent forms in gene-banks.

THE UTILIZATION OF CEREALS

The various cereals, whatever their origin, have come to be the most

important of all types of food crops. They have spread to almost all parts of the world, and it is only in wet tropical areas, where seed production of any kind is difficult, that they are less important than vegetative storage-organ crops such as cassava and yams. They are now grown each year on something over seven hundred million hectares, that is on about one twentieth of the total land surface of the globe.

The cereals are all similar, in that they all produce food suitable for man and animals, relatively easily grown, harvestable at a single operation, and relatively easily stored. In all of them it is the caryopsis which is the valuable part, and grain yield is the important feature; in maize this may be about 60% of the total above-ground yield, in wheat about 40%, but in some of the less developed millets only about 10%. There are relatively small differences in caryopsis structure and composition between the different cereals. The percentage by weight of the combined pericarp and testa varies from about 3 to 8, that of the endosperm from about 82 to 94 and of embryo from 2·5% to about 12. In average chemical composition the range is from about 66 to 73% carbohydrate, mainly starch, 10 to 13% protein, 1·5 to 6% oil and 1 to 2% fibre. The cereals are thus, from a nutritional point of view, largely interchangeable, and the utilization of a particular species is determined by climatic and cultural requirements and by food preferences. In a large part of the world bread is the preferred cereal food; only in wheat, and to a lesser extent in rye, are the proteins of the endosperm suitable for bread making, and wheat therefore largely replaces other cereals in all areas where it can be grown. Wheat and rye have the further advantage for human consumption that they are available in satisfactory naked forms, in which the caryopsis threshes out cleanly, but does not readily shed before harvest. Rice, requiring a hot climate and abundant water, comes second to wheat in world importance, and is the prefered food of large populations in eastern Asia. It cannot of course be used for bread; it has the disadvantage that no naked forms exist, but this is overcome by processing after threshing. The third place is occupied by maize, which has spread from its original American area to all the warmer regions of the world. Maize is a plant of very high photosynthetic efficiency under warm conditions, but the grain although free threshing is again not suitable for bread and a large proportion of the total yield is used for animal feeding. Barley is the second most important cool-temperate cereal, grown mainly for malting and since the middle of this century extensively for animal food; it is used in naked forms for human food only in areas such as Central Asia where wheat will not grow. Oats, not available in very satisfactory naked

Table 1. Comparison of cereal species.

Figures are approximate and vary with cultivar and with sample; those for areas and yields are for mid-1970s. Figures in brackets are for caryopsis only.

	WHEAT	BARLEY	OATS	RYE	MAIZE	RICE	SORGHUM	MILLET
Tribe	Hordeae	Hordeae	Aveneae	Hordeae	Maydeae	Oryzeae	Androp^{ae}	Paniceae
Origin	S.W. Asia	S.W. Asia	S.W. Asia	S.W. Asia	America	S.E. Asia	Africa	Asia, Africa
Climatic requirements	Temperate	Temperate	Cool	Cool	Warm	Warm wet	Warm dry	Warm dry
World area (million ha)	200	60	45	30	100	180	50	40
World average yield (t/ha)	1·3	1·4	1·4	1·1	2·0	2·0 (1·2)	1·0	0·5
U.K. area (thousand ha)	1 100	2 400	240	6	1	–	–	–
U.K. average yield (t/ha)	3·8	3·4	3·4	3·1	4·5	–	–	–
Average yields elsewhere					4·8	6·5 (4·4)	2·6	1·3
Grain								
Length (mm)	5–8	8–12	6–14	6–10	8–17	5–11	3–5	1–3
Weight (mg)	50	46	40	30	280	30	23	8
Number per kg (thousands)	20	22	25	33	3·5	33	44	120
Components of grain %								
Lemma and palea	–	13 (–)	25 (–)	–	–	20 (–)	–	+
Pericarp and testa	8	3 (3·3)	9 (12)	10	6·5	5 (7)	8	
Aleurone	7	5 (6)			2·2			
Starchy endosperm	82	76 (88)	63 (84)	87	80	73 (91)	82	
Embryo	2·5	3 (3·4)	2·8 (3·7)	3·5	11·7	2·2 (3)	10	
Analysis of grain % (air dry								
Carbohydrate	68	67	58 (66)	70	70	63 (73)	72	64
Protein	12	10	10 (13)	12	10	8 (10)	13	12
Oil	2	2	5 (6)	1·5	4	1·9 (2·4)	3·2	3·4
Fibre	2	4·5	10 (1·2)	2	2	9 (1·1)	1·8	8
Ash	1·6	2·6	3 (1·9)	2	1·4	6·3 (1·6)	1·7	3·4

forms, is grown mainly for animal feeding in cooler more humid areas than wheat; rye is largely confined to cool areas where soil conditions are too poor for wheat. Sorghum and the millets are used mainly in warm areas too poor for maize or too dry for rice.

Cereals in Britain

Wheat, in its more primitive forms, reached Britain in the fourth millenium B.C.; it was partly replaced by barley in the second millenium but improved forms became important in the first millenium and early in the historic period oats and rye were added. All these four cereals were grown during the Middle Ages and when necessary pressed into service for bread making. With improved standards of

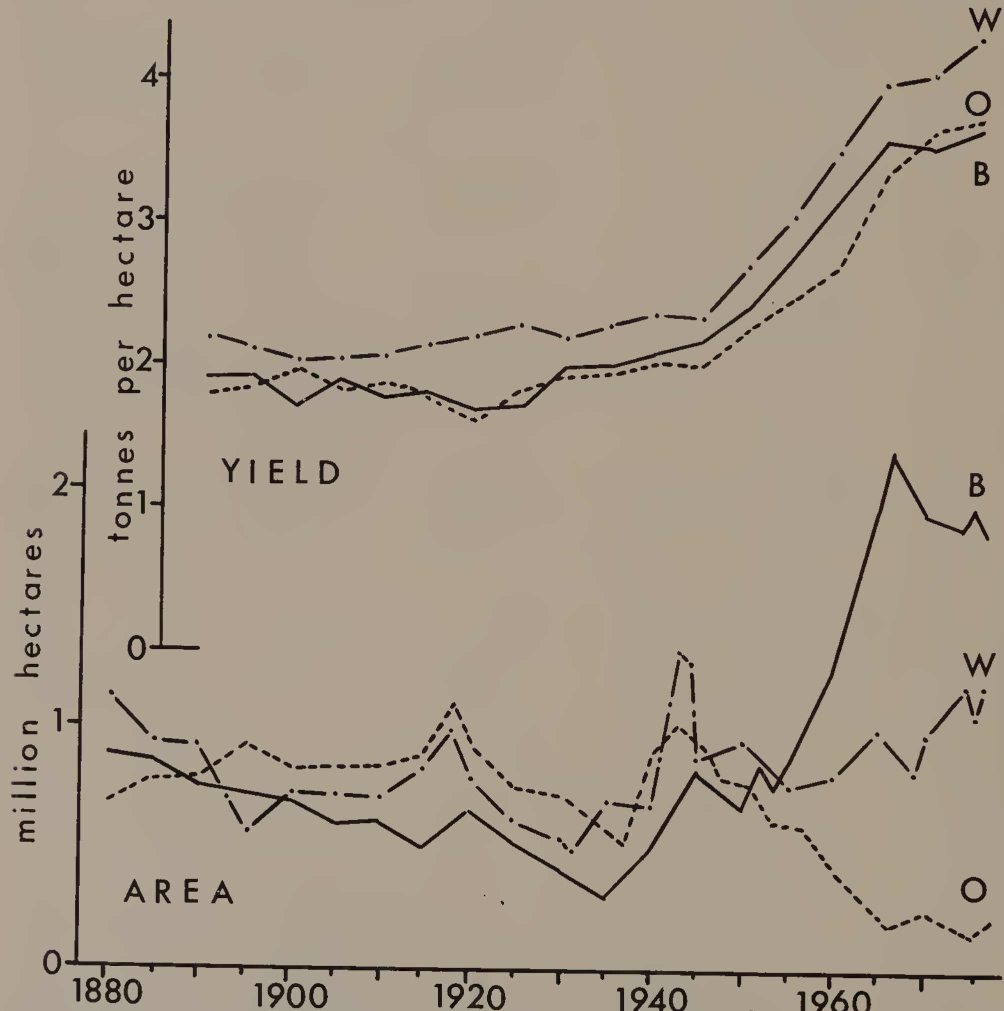


Fig. 16. Yields and areas of the three common cereals in England and Wales during the past hundred years. W, wheat; B, barley; O, oats. Yield curves are based on five-year averages, and area curves have been similarly smoothed to exclude minor year-to-year fluctuations.

agriculture rye tended to fall out of use, and by the nineteenth century wheat, the main bread corn, barley, mostly used for malting, and oats, primarily grown for horses and so providing the main motive power in agriculture and transport, occupied roughly equal areas. Apart from fluctuations caused by the necessity for increased production during times of war, the area devoted to wheat has remained approximately constant, increased demand being met by increased importation. Barley remained at about the same level until the 1940s, when the introduction of more easily grown varieties, and the development of the use of this cereal for animal feeding resulted in a doubling of the area within twenty years. The replacement of horses by tractors and mechanical transport removed the main purposes for which oats were grown and the rise in barley area was at the expense of oats. It should be remarked that these changes were primarily due to alterations in demand; there is little difference in yield between these cereals, and for all of them the yields per hectare have roughly doubled since 1900. Two other cereals are at present cultivated in Britain to a smaller extent; these are rye, grown as a herbage plant for early spring grazing and also as a special-purpose grain crop on contract, and maize, which can be grown as a grain crop in the warmer south-east, but which is more widely grown as a silage crop throughout the southern half of Britain.

The extensive mechanization of cereal growing since 1940, and the consequent removal of hedges to give larger more economically worked fields, combined with the development of efficient selective herbicides and the increased availability of artificial fertilizers, has resulted in a change from traditional mixed farming. Rigid rotation of crops has become less necessary, and in many areas almost continuous cereal growing has become economically desirable. This has accentuated the disease problem and there has therefore been an increased demand for cultivars of the various cereals which are genetically resistant to the more important diseases, and also for break crops which, while unaffected by cereal diseases and therefore effectively checking their build-up, can be cultivated and harvested with the same equipment as the cereal crops.

THE CULTIVATION OF CEREALS

Life-history and behaviour under field conditions

The life-history of annual grasses has been discussed (p. 36), but it must be emphasized that the behaviour of plants grown under the

close-spaced conditions of a cornfield is different from that of plants grown without competition.

The behaviour of a true winter wheat may be taken as an example. If sowing takes place in early November, germination may be complete in early December; leaves of the main shoot appear in succession through January and February, the first side tiller being visible towards the end of February at about the same time as the fourth leaf. Further leaves and side tillers appear during March, April and May if spacing is sufficiently wide to allow of this amount of tillering. Early in April the apex of the main shoot shows the first rudiments of the inflorescence and the same change from the vegetative to the fertile stage may occur in the apices of the first few tillers shortly afterwards. From the point of view of yield it is important that the inflorescence rudiments should be large, since they will determine the final size of the inflorescence. No further leaves or tillers are produced on a shoot once its apex has changed, although those already laid down will develop. Competition by the developing inflorescence for assimilates is so strong that the later-appearing tillers never reach the inflorescence stage, and are usually dying off in May. Meanwhile, development of the inflorescence of the earlier-formed tillers continues, with florets forming successively from the base of each spikelet during May; in wheat up to nine florets per spikelet may be formed, of which the ninth develops for only one day, the eighth for rather longer, and so on, so that usually only four or five florets per spikelet reach maturity, the others remaining rudimentary. Growth of the stem internodes takes place in the fertile tillers, so that eventually the inflorescence becomes visible above the uppermost leaf-sheath. This emergence of the ear usually takes place during the middle of June; the ear of the main tiller emerges first, but there is a relatively quicker growth of the side tillers, where spacing is wide enough to allow these to develop, so that although the latest-formed tiller to produce an ear may not have become visible until nearly three months after the appearance of the main shoot at germination, its inflorescence emerges within at most from two to three weeks of that of the main shoot. This tendency for all ears to emerge at about the same time under field conditions is of great importance, in that it results in an evenly-ripening crop; if cereal plants are grown at wide spacing, so that there is less competition, and a large number of tillers are able to develop an ear, it will often be noticed that the ears of younger tillers are still green when those of older ones are ripe. The same effect can be seen under field conditions if ears develop on younger tillers, as, for instance, in an oat crop attacked by frit-fly in which the earlier-formed tillers are killed.

Flowering occurs some ten days after emergence of the ear in wheat, and although individual florets remain open for less than an hour, the whole process may be spread over a week or more for all the florets of any one ear. In wheat, barley and oats, self-pollination is the rule, with pollen shed on to the stigma before the floret opens; in rye a considerable amount of crossing takes place. Fertilization takes place within a few hours of pollination, and embryo and endosperm develop; starch begins to appear in the endosperm some ten days after fertilization and increases in quantity partly owing to the photosynthesis of the ear itself, partly by translocation from the leaves. It is mainly the two upper leaves which are concerned. Adequate leaf area of individual shoots is important in the early stages to ensure large inflorescences, so that there is an adequate number of developing grains to store the assimilates produced at this post-flowering stage. For high yields this must be combined with a large and persistent photosynthetic area of ear and upper leaves. By about a month after fertilization, the water content of the grain ceases to increase, and a few days later the grain reaches its maximum size. The embryo is mature and becomes dormant, and desiccation of the grain begins, and the endosperm becomes harder, passing through 'milk-ripe' to the fully ripe, hard stage. Meanwhile, gradual death of the whole plant, from the roots upwards, has taken place. In most cereals, breaking-up of the inflorescence to set free the grain takes place readily when the dead-ripe stage is reached, or the straw becomes brittle so that whole ears are lost. Although such shedding is very much less rapid and less complete than in wild forms, it is still necessary to take precautions and select varieties which do not shed readily when ripe; this is important with crops which are to be combined and which must therefore be left standing until fully ripe.

Dormancy of grain. The embryo, which has shown rapid development during the early stages of caryopsis formation, ceases growth and shows no further changes during the later stages of ripening. Germination involves the restarting of active growth of the embryo; this is dependent on a supply of water, and germination normally starts when the mature grain is soaked. In the cereals, however, the freshly-ripened grain may show a period of dormancy, during which germination will not take place, even when ample water is supplied. This dormancy is not due to any immaturity of the embryo, nor (as in 'hard' seeds of *Leguminosae*) to failure to absorb water, but is dependent on the character of the outer layers of the grain, which at this stage may prevent an adequate oxygen supply to the embryo. Where the caryopsis is closely invested by lemma and palea, as in

barley and oats, these may have some effect, and their removal may reduce dormancy, but it is primarily the pericarp and testa which are important and dormancy can be broken by removing or puncturing them. This effect of the pericarp and testa is a transient one, and dormancy of the freshly-ripened grain is therefore only temporary. Its duration varies in different species and in different varieties, and its length is of considerable agricultural importance, If it is very short, grain in the ear may germinate if it is wetted, so that in a wet harvest much of the yield may be lost by sprouting of standing or sheaved corn; while if it is very long, the value of the grain for sowing or malting will be reduced.

Factors affecting yield under field conditions

(1) *Time of sowing.* Inflorescence production in the grasses is largely controlled by day-length; the temperate cereals are long-day plants which change from the vegetative to the flowering stage when a certain length of day is reached in spring. Alteration of time of sowing, therefore, does not greatly alter time of flowering and harvest for any particular variety, and late sowing will tend to give a low yield at about the normal harvest time, owing to reduction in the total photosynthesis, rather than a normal yield at a later date. In winter varieties of wheat, rye and barley the position is complicated by the fact that a cold period is necessary before the plants can respond to increased length of day; if such varieties are sown in spring they do not flower in the year of sowing, but make vegetative growth only and flower the following year. The stage of growth at which the low temperature occurs is not important, and Russian work has shown that it can be effective before the corn is sown. Storage of the dry, dormant grain at low temperature has no effect, but if just sufficient water is added for the embryo to become active, and the moist grain then stored for several weeks at a temperature a little above freezing-point, the treatment is effective. The treated grain, if then sown, will develop and flower without any further cold period. This conversion of a winter variety into a spring form is known as *vernalization*; while it is of considerable theoretical interest, it is of no economic importance in this country.

In general, the winter varieties, with their longer growing period, are higher-yielding than the spring forms, but the difference is usually not great. It is, of course, essential that winter varieties shall be sufficiently hardy to withstand the winter climate; thus, for example, winter oats, which do not show a very great resistance to hard winters, are rarely grown in northern England or in Scotland. Winter wheats

can be grown throughout the British Ises, but only certain varieties are hardy enough for use in Sweden, while in the greater part of the Canadian wheat area only spring varieties can be used. While true winter varieties, which have a definite low-temperature requirement, cannot be sown in spring, the reverse, sowing spring varieties in winter, is satisfactory if they are sufficiently hardy, and spring barleys, for example, are sometimes winter-sown in southern England.

The optimum date of sowing varies not only according to district but also with the variety. The older cultivars of winter wheat had a large cold requirement, and needed to be sown early; most modern winter wheats have a smaller requirement and can safely be sown in early spring. In barley the time of sowing is often important in determining the incidence of disease.

The tropical cereals are mainly short-day plants, and their season of growth in the tropics, with uniform short day-length throughout the year, is largely controlled by temperature and distribution of rainfall. They are, of course, not frost-hardy, and have a high minimum temperature for germination, so that the effective growing season in Britain would be extremely short. The hardier forms of millet could be grown in southern England, but would not be economic; maize for grain is confined in Britain to the warmer south-east, and it is only the quicker-maturing and therefore relatively lower-yielding varieties which will ripen.

(2) *Plant population and spacing.* Cereals, like most other crops, are grown in such a way as to give the maximum yield per hectare, not the maximum yield per plant. All the cereals (with the partial exception of maize) are capable, in the absence of competition, of tillering to produce numerous shoots. These tillers however are initially produced at the expense of the parent shoot, and there is little compensatory return transport of the assimilates which they later produce. The main shoot is thus smaller in a multi-tillered plant, and as a consequence the inflorescence initial smaller. This young inflorescence is the sink to which the products of later post-flowering photosynthesis will be translocated, and if it is small photosynthesis will be reduced, and with it the yield of grain. The yield of grain from a given area will therefore be greater if it is derived from numerous plants, each with a single shoot or at most a few shoots, than if the area is occupied by a few plants each with numerous shoots, some of which fail to produce an inflorescence. High tillering capacity is thus of little importance in cereals, providing that conditions are perfect. However, if drilling is not completely regular, so that some plants are widely spaced, or if conditions are such that some main shoots, or

some whole plants, do not survive, then high tillering capacity is valuable, since side tillers will fill the vacant spaces and give at least partial compensation. The more adverse the conditions or the lower the standard of cultivation, the more important will tillering capacity be; it is because of rising agricultural standards that less emphasis is now placed on tillering capacity than was formerly the case. Modern temperate cereal cultivars, although tillering less than the older cultivars, still retain enough tillering capacity to compensate for likely departures from ideal conditions.

Plant population is of course controlled by seed-rate, and under most conditions seed-rate and yield are connected by a flat-topped curve. Initially yield rises rapidly with increased seed-rate and then gradually less and less rapidly until a ceiling yield is reached, and then with further increases in seed-rate the yield slowly begins to decline. The initial phase of rapid rise would correspond with the increasing number of plants giving an increasingly complete leaf canopy, and hence increasingly complete light interception, the flatter part of the rising curve to the increasing change from multi-tillered to single or few shoot plants, and the decline phase to increasing competition between single shoot plants becoming severe enough to reduce inflorescence production. The seed-rate for ceiling yield may not be the optimum seed-rate, since at the level corresponding to the flat top of the curve, a given weight of extra seed may produce a smaller increase in grain yield. The grower really requires the seed-rate which will give, not the maximum crop, but the maximum difference between seed harvested and seed sown. This seed-rate will be rather less than that for maximum yield, and if yield is looked at in terms of value may be much less if the seed corn is more costly than the produce.

Since small alterations in seed-rate have little effect on yield it is not usually considered necessary to take into account any variations in seed size, i.e. in number of grains per kilogram, although this is recommended in some continental systems of intensive wheat growing. In addition to plant population the actual spacing of plants may also affect yield; for example drilling at 10 cm between rows may give higher yields than the same seed-rate drilled at 17 cm. Precision drilling with grains 2·5 cm apart in the rows may give further improvement, and it has been suggested that plants spaced at say 5 cm square might, if it were practicable, be even better.

(3) *Soil fertility.* Cereals vary considerably in their soil-fertility requirements, with rye most tolerant of low fertility, and wheat and maize needing the most fertile conditions. In general there has been a continuous progress towards forms suited to high fertility levels; the

modern cereal species are mainly less suited to poor conditions than the more primitive species, and within the species, modern varieties have a higher fertility requirement than the older ones. Rye and oats are tolerant of somewhat acid soils, but wheat and barley need adequate lime. Application of phosphate and potash may be necessary, but the most conspicuous response is usually to nitrogen. The addition of 1 kg/ha nitrogen gives in general an increase of some 12 kg/ha of grain, and this order of increase may continue up to a total application of nitrogen of some 100 kg/ha. Higher applications may sometimes be desirable, but very high nitrogen levels may give rise to an excessively dense canopy, leading to reduced grain filling on account of increased competition for water and light, and to increased disease susceptibility. Increases in nitrogen application are in practice, however, mainly limited by the standing ability of the plant.

(4) *Standing ability.* It has been seen that increased yield per acre in cereals is due mainly to increased weight of the individual inflorescence; this inflorescence is borne on a comparatively long, slender culm, and the full potential yield can only be obtained if this culm is strong enough to carry it. In addition to the weight of the ear, the culm also has to withstand the additional weight of water standing on the ear in wet weather, and the beating effect of heavy rain and wind. There may be some recovery from bending-down of the culm (*lodging*) if this occurs at an early stage; the nodes of the stem retain their meristematic activity after growth of the internodes has ceased and respond to the geotropic stimulus of laying by one-sided growth, so that the upper internodes resume a more or less vertical position. If, however, lodging takes place later, or if breaking of the culms is involved, no recovery can be expected. Lodging may cause very serious reduction in yield; grains may fail to 'fill' completely and will ripen slowly and incompletely and, if badly laid, may sprout or rot under wet conditions. Harvesting is more difficult and expensive, and rarely as efficient as with standing corn.

Standing of a crop is partly a function of the individual cereal variety, and partly of the cultivation conditions. The standing ability of the plant depends on its shape and on the character of the straw. Winter varieties of the common cereals tend to be prostrate in the early stages, so the lower internodes of the culms are almost horizontal; this gives a broad-based plant somewhat less readily laid than the narrow-based erect spring type. Much the same effect is produced in maize, where the rigid upright stem is supported by *prop-roots,* which grow outwards and downwards from the nodes immediately above ground level. The characters of the straw which affect standing ability

are its length and its strength. Long straw provides more leverage for the beating action of wind and rain, and short-strawed varieties are therefore much more resistant to lodging. Strength of straw varies considerably; it is mainly controlled by the amount of thickening and lignification of the cells of the ground tissue. Straw diameter and size of the internal cavity (*lumen*) also affect strength.

The main factors affecting the ability of any given variety to stand in the field are the supply of soil nutrients and the density of the crop; the actual amount of lodging which occurs will depend largely on weather conditions. Severe storms may, of course, beat down any crop, and standing ability must be assessed in relation to normal weather conditions to be expected at harvest and during the preceding few months. The presence of weeds and of disease may also have an important influence on standing.

The main soil nutrient influencing standing is nitrogen; high nitrogen not only increases the weight of inflorescence to be supported, but also decreases the strength of the straw. With a high nitrogen supply the straw tends to be longer, and is also more succulent; this may be particularly marked if the manuring is unbalanced, with an excess of nitrogen. The level of nitrogen supply is thus the preponderating influence, and from a practical point of view the cereal varieties can be classified into those suitable for low, medium and high nitrogen levels, and in general the highest yield will be obtained by growing a cereal at the highest level of fertility at which it can be relied on to remain standing.

Density of crop influences lodging mainly by its effect on the light reaching the developing culm. A high seed-rate will give a larger number of tillers in a given area, even after allowing for the compensating effect of reduced percentage establishment and reduced number of tillers per plant. The light reaching the base of tillers will thus be reduced, and partial etiolation occur, giving more elongated, thinner and less lignified stems. The presence of weeds may have the same effect, and external shade from trees or tall hedges may also result in weaker straw and consequent lodging.

Any disease which weakens the straw is likely to result in increased lodging; the most important in Britain is Eyespot, caused by the fungus *Pseudocercosporella herpotrichoides*, and genetic resistance to this is an important consideration in the breeding of wheat cultivars. In all the cereals increase of standing ability has been a major factor in the increase of yields during this century. This has been achieved so far mainly by progressive reduction of straw length; the point has now perhaps been reached where further improvement will depend on increases in straw strength.

5

CEREALS: SPECIAL

WHEAT

Wheat belongs to the genus *Triticum*; this is a member of the tribe *Hordeae,* and is closely related to *Agropyron.* The inflorescence is a typical spike, with a single spikelet at each node. Each spikelet consists of a pair of rather stiff glumes, and from two to nine florets borne on a very short rachilla; the upper one or more florets being sterile. The glumes are of about the same size as the lemmas, keeled and asymmetrical, with the side away from the rachis larger. The lemmas are of thinner texture, awned or awnless; the large caryopsis is hairy at the apex, and in some species threshes out from between the lemma and palea. Leaves usually hairy, with hairy auricles. All species annual.

The genus *Aegilops* (known, from the fancied resemblance of the spikelets of some species to a goat's head, as goat-faced grasses, or goat grasses) is very closely related to *Triticum,* and some authorities treat it as a section of this genus. It differs in having the glumes not keeled and bearing a number of awn-like points. Usually the glumes are stiff and tightly wrapped around the florets, so that although the caryopsis is fairly large, the *Aegilops* species have not been exploited as cereals. They will however cross with *Triticum,* and in fact all the important wheats are *Triticum* × *Aegilops* crosses.

Very many distinct types of wheat exist which have been named as species. They are separable into three groups: diploid, tetraploid and hexaploid. It would perhaps be most logical to regard these three groups as the species, and the types within them as subspecies, and this is sometimes done. The diploid wheats are then treated as subspecies of *Triticum monococcum,* the tetraploids as subspecies of *T. turgidum,* and the hexaploids as subspecies of *T. aestivum.* For convenience, however, the traditional nomenclature is used here, and each group regarded as consisting of a number of species, some wild, some cultivated.

DIPLOID SPECIES

Triticum boeoticum Boiss. (*T. aegilopoides* Bal.). **Wild Small Spelt**

Stem slender, hairy at nodes. Rachis very fragile, whole spike breaking up very quickly at maturing. Spikelets 2–3 flowered, lower 1–2 florets maturing grain. Glumes tough, long, lemmas awned, caryopsis long narrow. Wild in hilly areas in sparse woodland from Greece to western Iran; now spread as weed of cultivated fields, primary area probably more restricted. Occurs in two forms: subsp. *aegilopoides* (Link.) Schiem., slender, strictly one-grained, in western part of range; and subsp. *thaoudar* (Reuter) Schiem., more robust, often two-grained, farther east. Primary stands exploited by Natufians (p. 44) and brought into cultivation. Diploid, with two sets of seven chromosomes known as AA.

Triticum monococcum L. **Small Spelt** or Einkorn

Similar to *T. boeoticum* and derived from it in cultivation. Rachis less fragile, not breaking up except on threshing. Inflorescence denser, broader, less hairy; much narrower in face view than in side view, so that at first glance it looks more like a two-rowed barley than a cultivated wheat. In cultivation at Jericho and in south western Asia Minor from *c.* seventh millenium B.C. and widespread later, mainly in hilly areas, but never very important and often only in casual mixture with the better *T. dicoccum* (see below); now almost obsolete. (Spelt is a general term for wheat in which the caryopsis does not thresh out.)

TETRAPLOID SPECIES

Triticum dicoccoides Körn. **Wild Emmer**

Rather similar to *T. boeoticum,* but inflorescence stouter, less flattened. Rachis very fragile. Spikelets 2–3 flowered, with 1–2 grains, larger than in *T. boeoticum.* Wild, with more restricted and more southerly range than *T. boeoticum,* extending from Palestine to western Iran in hill steppe and open woodland; not spreading as a weed. Apparently exploited as a wild cereal and brought into cultivation in the same way and about the same time as *T. boeoticum.*

Tetraploid, with chromosome sets AABB, that is with fourteen chromosomes which are those of *T. boeoticum,* and fourteen derived from another species by amphidiploidy; that is simple crossing between the two species giving a sterile diploid AB which on chromosome doubling gives the fertile tetraploid AABB. The most likely

source of the BB genome appears to be *Aegilops speltoides* Tausch; this is a diploid annual, normally cross pollinated, with a more strictly Mediterranean and more lowland distribution, but with a primary range overlapping that of *T. boeoticum*. Its genome, SS, is however not identical to the BB chromosomes of *T. dicoccoides,* and to give rise to this species must have been somehow modified, either by mutation or perhaps by partial interchange with other species. In 1978 *T. searsii,* a newly described species from Israel, was reported as the source of the B genome.

Triticum dicoccum Schülb. **Emmer**

Resembling wild emmer, but inflorescence larger, denser, less hairy. Rachis less fragile, breaking up only on threshing. Spikelets 3–4 flowered, two-grained. Evidently derived from *T. dicoccoides* by cultivation, and transitional forms have been recorded from Jarmo (N.E. Iraq) dated to the seventh millenium B.C. A better, higher-yielding wheat than *T. monococcum* and better adapted to lowland conditions, so that its cultivation became much more widespread; emmer was the main wheat in Egypt and Mesopotamia, although primarily adapted to a Mediterranean climate it also spread northwards through Europe with the spread of neolithic cultures, and was the first cereal to be grown in Britain. It was the most important species of wheat up to Roman times, being then largely replaced by the more convenient naked wheats; some cultivation persisted in Europe, Ethiopia and India in areas where its marked drought resistance was of value. A range of forms exists, and some are still cultivated on a small scale. (*T. georgicum* Dek. is a similar but denser form still cultivated to a small extent in southern Russia; *T. timopheevi* Zhuk., a broad-eared form probably of slightly different origin with chromosomes AAGG where G is perhaps a modification of the S genome of *Aegilops speltoides* different from the B of *T. dicoccum,* is found as a weed, perhaps a relic of former cultivation, in the same area.)

Free-threshing tetraploid species

Emmer has the disadvantage of a fragile rachis and consequent absence of the free-threshing naked caryopsis character. There are however some free-threshing tetraploid species and these are still in cultivation as special-purpose wheats. Their origin is uncertain and no intermediates are known; they may have arisen from emmer by mutation, but there is no evidence for their early use, and they may

derive their free-threshing character from crosses of emmer with bread wheat (*T. aestivum*, p. 65). They retain however the essentially Mediterranean character of emmer.

Triticum durum Desf. **Macaroni Wheat**

Inflorescence large, rachis tough, spikelets 5–7 flowered, 2–4 grained. Lemmas with large stiff awn. The caryopsis is large, somewhat triangular in cross section, with very hard flinty endosperm; it threshes out from the lemma and palea which remain attached to the tough rachis. Macaroni wheat is higher yielding than emmer, although not equalling bread wheat in yield. Its very hard endosperm is not very suitable for bread making, but is particularly adapted to the making of macaroni and similar pasta products, where the wheat is ground to a fine semolina which is made into a stiff unyeasted dough, extruded through nozzles and then dried. It is widely grown in Mediterranean areas for this purpose and commands a higher price per tonne than bread wheat. Field-scale trials of French cultivars of *T. durum* in eastern England were proposed in 1978. (*T. pyramidale* Perc., Egyptian Cone Wheat; *T. turanicum* Jakub. (*T. orientale* Perc.), Khorasan Wheat; *T. carthlicum* Nevski (*T. persicum* Vav.); and *T. ispahanicum* Heslot are localised related forms.)

Triticum polonicum L. **Polish Wheat**

A species closely related to *T. durum* and probably derived from it by mutation, but very different in appearance owing to its very long lanceolate almost leaf-like glumes. Caryopsis very long, flinty. A form of little importance, having no real advantages over *T. durum*. Occasionally cultivated for macaroni in the Mediterranean area; not Polish in origin, nor grown there.

Triticum turgidum L. **Rivet Wheat**

Inflorescence very large, rachis tough, caryopsis threshing out, spikelets 5–7 flowered, 3–5 grained. Glumes short, broad, lemmas strongly awned, caryopsis short, plump with a marked dorsal ‘hump’, endosperm soft, opaque, not well suited to bread making; used for biscuits or in mixture with better wheats for bread. Cultivated to a small extent in Mediterranean areas and a rather hardier form in southern England up to the 1950s. Until then rivet (latterly mainly the variety Rampton Rivet) was the highest-yielding wheat for use on poor heavy land.

Fig. 17. Rivet wheat (*Triticum turgidum*). A, spike in face view, $\times\frac{1}{2}$. B, single spikelet and separate parts, $\times 3$. A, awn. C, caryopsis. G, glume. L, lemma. P, palea. R, rachis.

Rampton Rivet was a winter wheat with very large bearded ears, square in cross section and with hairy bluish-grey chaff. The very long straw was semi-solid, wiry, and bent freely so that the mature ears were pendulous; the grain was red, and rather firmly held, and thus perhaps more birdproof than bread wheats. Rivet had a long growing season, required October sowing and even then was late maturing.

Crosses between *T. turgidum* and *T. durum* are possible, and such hybrids may be of value.

HEXAPLOID SPECIES

The most important wheats today are hexaploids. These have six sets of chromosomes AABBDD, that is those of emmer plus a further two sets which have been shown to be derived from another goat grass species *Aegilops squarrosa* L. This is a diploid annual, primarily of steppes and open forest but spreading as a cereal weed; it shows a wider ecological and climatic range than *A. speltoides,* and occupies a

more easterly and northerly area, extending along the southern fringe of the steppes from the southern end of the Caspian Sea to Afghanistan and Turkestan. Its primary range does not overlap that of *Triticum dicoccoides,* and the probability is that the cross took place with *T. dicoccum* when the cultivation of this spread into the *A. squarrosa* area, or when the latter spread as a weed into fields of cultivated emmer. With one minor exception all the hexaploid wheats are cultivated forms, as would be expected if they arose in cultivation in this way. It is of course likely that the natural crossing to give the sterile triploid ABD and ensuing natural chromosome doubling to give the fertile hexaploid took place on a number of occasions.

Although the chromosomes from the three original parent species are very similar, there is normally in the hexaploids no association or interchange of genetic material between the three groups. The hexaploids thus behave genetically as though they were diploids, and selfed heterozygous forms give progeny segregating in normal diploid mendelian ratios. This ‘diploidization’ is due to a gene on chromosome 5B (i.e. on the pair of homologous chromosomes derived from *A. speltoides* described for reference purposes as number 5). In the absence of this chromosome, or in the presence of a gene from another source which over-rides it, interchange between homoeologous chromosomes (e.g. between 1A and 1B, or between 3A and 3D) is possible; this mechanism has sometimes been made use of in recent scientific wheat breeding.

The hexaploid wheats are not only, in most cases, larger and higher yielding than the diploids and tetraploids, but they inherit from *A. squarrosa* the adaptibility to a much wider range of climatic conditions; they are no longer essentially Mediterranean plants as were the diploids and tetraploids.

Hexaploid spelt wheats

Triticum spelta L. **Large Spelt**

Rachis fragile, breaking below spikelets on threshing, caryopsis not threshing out. A very distinct-looking wheat with narrow widely spaced spikelets and square topped glumes. Spikelets 3–4 flowered, 2–3 grained. Lemmas awned or awnless.

This is the most important of the hexaploids in which the caryopsis does not thresh out; it is essentially a mountain form, resistant to continued snow cover of the young plant, and may have originated in Europe, since there are no records of its presence in south western Asia. Apparently in fairly widespread cultivation in central Europe in

the Bronze Age, spreading to Britain in the early Iron Age and then being replaced by bread wheat. Still cultivated to a small extent in south western Germany and Spain; requires special milling treatment, and the caryopsis is used mainly in the same way as pearl barley, rather than as flour.

The other hexaploid species which are not free threshing are of minor importance. *T. macha* Dek. et Men., with rachis breaking above the spikelets, is cultivated to a small extent in Georgia (U.S.S.R.). Its var. *megrilicum* Dek. et Men. is a wild form with a very fragile rachis shattering readily; its status is uncertain, but it is a very localized form, and unlikely to have been the ancestor of the other hexaploids. *T. vavilovi* (Tum.) Jakub., from the same area, has large ears with lax rachilla.

Free-threshing hexaploid species

Triticum compactum Host. **Club Wheat**

Inflorescence short, dense, rachis tough. Spikelets crowded, 6–7 flowered, with 3–4 grains; caryopsis small, free threshing.

Apparently the first developed of the free-threshing hexaploids; occasional naked grains found in admixture with emmer in neolithic prove, where identifiable, to be this species. It was however never cultivated as a main crop in south-western Asia or Egypt, but was sporadic all over Europe during the Bronze Age, becoming increasingly used in the Iron Age, and was largely replaced by bread wheat in early historic times. Now only occasionally cultivated. (*T. sphaerococcum* Perc., Indian Dwarf Wheat, is a rather similar form with short rounded flinty grains, cultivated in India.)

Triticum aestivum L. (*T. vulgare* Host.) **Bread Wheat**

Rachis tough, caryopsis threshing out. Spikelets 5–9 flowered, with up to five grains. Inflorescence varying in size and density in different forms; glumes rather short, usually not keeled to base, red or white, glabrous or hairy; lemmas awned or awnless. Caryopsis large, plump but not humped, red or white; endosperm variable in texture, but less flinty than *T. durum*, less floury than *T. turgidum*; many forms suitable for bread.

By far the most important of all the wheat species; generally the highest-yielding and certainly the widest-ranging, as well as the one most suited to bread making. Perhaps derived by mutation from club wheat, but satisfactory evidence is lacking; the probable picture is that one or both of these species originated, either directly or via a

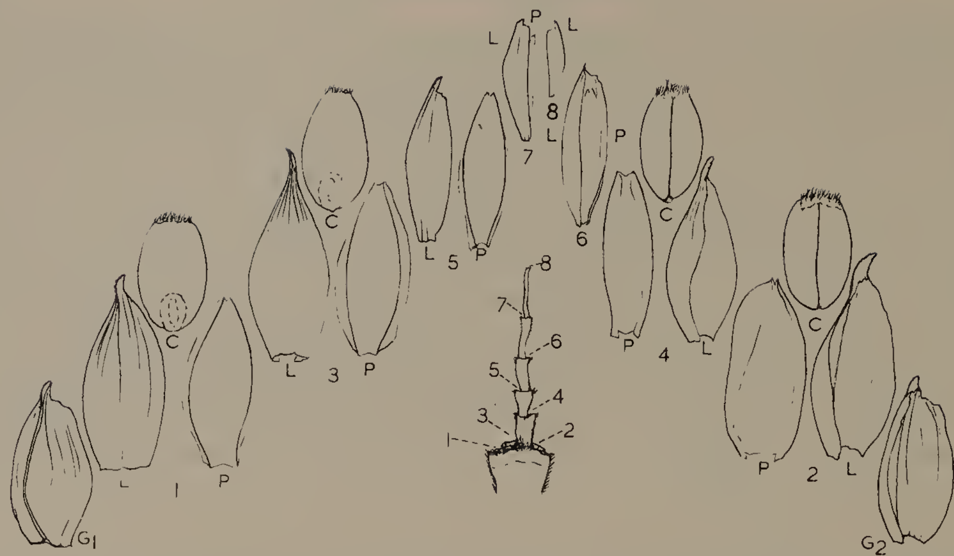


Fig. 18. Bread wheat, *Triticum aestivum* (var. Juliana); single spikelet separated into its constituent parts. The rachilla is shown in the centre, with the points of attachment of the eight florets numbered; the separated florets are numbered to correspond. Parts on left are shown in dorsal view, parts on right in ventral view; lodicules are omitted. G_1, G_2, glumes. L, lemma. P, palea. C, caryopsis (matured only in florets 1–4). ×2.

spelt form, from the crossing of emmer and *Aegilops squarrosa* somewhere south of the Caspian, but proved not to be particularly well adapted to climatic conditions there or in the Mediterranean area, and thus came into prominence only later, after wheat cultivation had spread to other more humid areas. During the past two thousand years it has come to replace almost all the other species, and has spread, in innumerable forms, to almost all parts of the world where any type of wheat can be grown.

RANGE OF BREAD WHEAT TYPES

The life history of a bread wheat has already been outlined (p. 52) and it need only be emphasized here that cleistogamous self-pollination is the general rule. Although chance out-crossing may very occasionally occur, it is too rare to have any marked effect during the normal life-span of a wheat cultivar. Cultivars thus remain distinct, each with a unique homozygous genotype, and an enormous range of types exists.

Winter and spring forms. Winter and spring forms differ in their cold requirement for vernalization. The older true winter wheats, used up to the early part of this century, in which the cold requirement was large, and which flowered normally only if sown in November or earlier are now obsolete in Britain. Modern winter

wheats have a smaller cold requirement and yield satisfactorily sown up to the middle or end of February. Alternative wheat cultivars such as Maris Ranger have an even smaller cold requirement and can be sown up to the end of March. Spring wheats have the smallest vernalization requirement, and may be sown in April. In general the winter wheats are more prostrate in the early stages and have a higher tillering capacity. Their longer growing season results in a higher yield, perhaps 20% above that of spring wheats. In Britain spring wheats form only some 10% of the total wheat crop, whereas in areas with very severe winters, such as many parts of Canada, winter wheats are insufficiently hardy, and only spring wheats are grown.

Straw characters. The flowering culm has normally about six internodes, of which the uppermost is the longest. This upper internode may be hollow with a large central lumen and thin walls, or semi-solid with a small lumen and thick walls, but since mechanical strength is provided largely by sclerenchyma, and this is formed only near the circumference, the difference has relatively little effect on straw strength. Total straw length varies from perhaps 60 to about 150 cm, but long strawed cultivars lodge readily and are suited only to soils of low fertility. With the increasing use of nitrogenous fertilizers and the change from harvesting by binder to combining there has been in Britain during this century a change to the use of progressively shorter cultivars. Extremely short-strawed forms derived from Japanese dwarf wheat are possible; the use of such derivatives has effected marked increases in yields in Mexico and in other areas of previously low yield. Opportunities for yield increases by this means in Britain, where yields are already high, are more limited; extreme dwarfing leads to problems such as those of diseases spread by rain splashing from the soil surface.

Ear characters. The ear is a spike of which the density varies from very lax, as for example in the obsolete cultivar April Bearded, with about 2 spikelets per centimetre length of rachis, to very dense as in the also obsolete Juliana, with 3·5 or more. Modern cultivars are usually intermediate in density. Spike length varies from about 5 to 15 cm, but tends to be to some extent inversely proportional to density, so that all forms have roughly the same number of spikelets, usually about 22 or 24. The uppermost spikelet is terminal on the rachis and is small and differs somewhat in shape from the remainder. The ear is roughly square in section, tapering lengthwise in some forms where the upper and the lower spikelets are less well developed than the central ones.

Fig. 19. Spikes of bread wheat, *Triticum aestivum*. A, face view, and B, side view of dense beardless variety (Juliana). C, D, lax bearded variety (April Bearded). $\times\frac{1}{2}$.

Ears may be bearded, where the lemmas are awned, or beardless. Cultivars now used in Britain are mainly beardless, or at most tip-bearded, that is with short awns ('scurs') on the uppermost spikelets only. Up to the introduction of the awned red-chaffed Highbury (recommended 1978) April Bearded, obsolete by about 1950, was the most recent British bearded wheat. Bearded wheats have some advantage, particularly under conditions of water stress, and are used in many parts of the world. It has been suggested that the introduction into bread wheat of the massive types of awn found in the tetraploids might result, by increasing ear photosynthesis as well as transpiration, in yields superior to those of beardless forms.

Chaff (glumes and lemmas) may be glabrous or hairy; hairy chaff tends to hold water and favour mould growth, and no hairy chaffed bread wheat has been used in Britain since the early part of the century. Colour of the chaff may be red (usually dull reddish brown) or white (pale yellow or 'straw'); this difference is visible only shortly before harvest, when the ear has 'turned colour'.

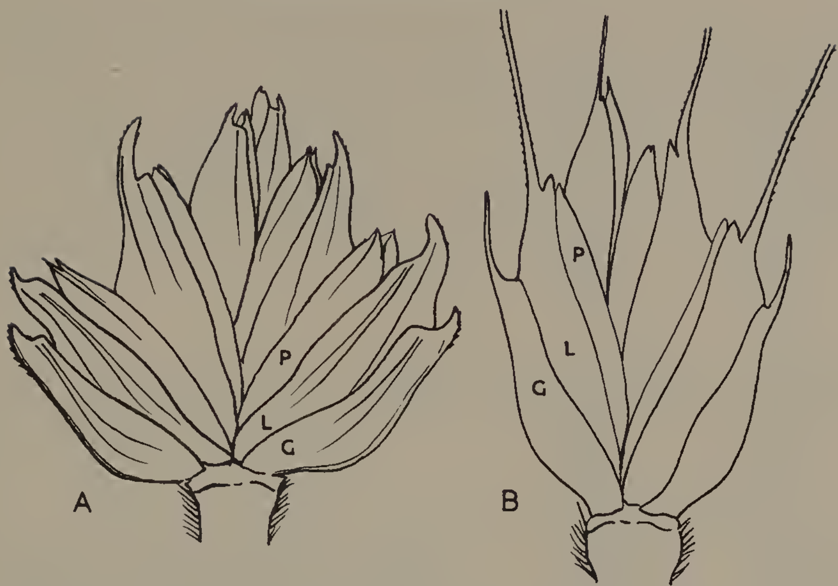


Fig. 20. Wheat. Single spikelet of A, a beardless variety (Juliana); B, a bearded variety (April Bearded); ×3. G, glume. L, lemma. P, palea.

Grain characters. Size of grain varies; in the larger winter wheats the caryopsis weighs about 60 g per thousand (for fully filled grains) while the thousand grain weight of the smaller spring wheats is about 40 g. In general large grains tend to be associated with high yield, but the correlation is not close. The N.I.A.B. Recommended Lists score wheat cultivars for 1 000 corn weight and for specific weight (apparent density of grain sample, expressible as kg per hectolitre).

Colour of the caryopsis is either red, of varying shades, or white; this colour is due to pigmentation of the testa, and although not in itself of great importance, since the testa is so completely removed by modern milling methods that its colour has little or no effect on that of the resulting flour, is closely linked with seed dormancy. The red-grained wheats display some degree of temporary dormancy at harvest time and show relatively little sprouting under wet conditions; the white-grained wheats do not show dormancy at this period and are therefore liable to very severe damage in wet harvest years. For this reason, no white grained wheats are now grown in Britain. There is some variation between different red grained cultivars; the N.I.A.B. Recommended Lists give scores for resistance to sprouting.

The character of the endosperm has a very marked effect on the suitability of the grain for milling and baking, and is discussed below in the section on quality (p. 71).

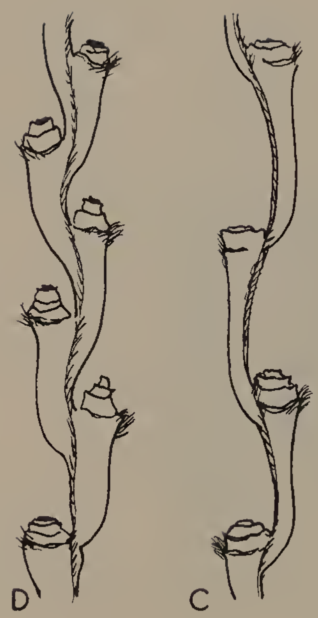


Fig. 21. Wheat. Part of rachis (in side view, with spikelets removed) of D, a dense-eared variety (Juliana); C, a lax variety (April Bearded); ×3.

Cultivar distinction

The total number of cultivars of bread wheat runs into many thousands, and the character differences discussed above will serve only to separate them into large groups. Each of these large groups has been given a Latin name as a varietas; thus all the beardless glabrous white-chaffed red grained cultivars are grouped as *Triticum aestivum* var. *lutescens* Körn.* However, all the wheat cultivars in the N.I.A.B. Recommended Lists from 1968 to 1977 answer this description, and would all fall into the one varietas. To distinguish between them it is therefore necessary to use a much wider range of characters.

The rules for the inclusion of a cultivar in a National List require that it shall be clearly distinguishable from all other cultivars on one or more important morphological, physiological or other character. Thus for this purpose any clear distinction, of whatever kind, is adequate, and cases have been recorded where wheat cultivars have been distinguishable only by differing iso-enzymes of alpha-amylase being present. Such physiological differences are acceptable, but morphological distinctions are much more convenient to deal with and this is of course particularly true where it is not a matter of

* For full treatment of this classification see Percival, *The Wheat Plant* under *T. vulgare*.

distinguishing a new cultivar from existing ones, but of determining that a given crop is the cultivar it purports to be, and that it is free from admixture, as for example in field inspection. Since wheat is self-pollinating all members of a cultivar are essentially homozygous and of the same genotype, and any genetic character that is not too much affected by cultural conditions can be used. Such differences are mainly small and of no direct economic importance. Characters used include:

Ear. Colour, density, shape, length of awns, special characters of apical spikelet, presence and frequency of supernumerary spikelets, hairiness of rachis.

Glume. Size, shape, characters of keel, beak, shoulder and base. Imprint (a semi-translucent area at base of glume, visible from inner side); large or small. Hairs on inner surface of upper part of glume: type 1, few and confined to inside of keel; type 2, hairs few but not confined to keel; type 3, whole of upper third of inner surface hairy.

Grain. Colour, size, shape, extent of brush area, prominence of embryo. The phenol reaction of the grain may be used, although the test is not suitable for use in the field. Soaked grains are wetted with 1% aqueous phenol and left exposed to the air; the colour (varying from unchanged to very dark brown) is observed after four hours. Alternatively pieces of grain may be stood on paper impregnated with catechol, which gives a similar reaction.

A complete but purely laboratory method which effectively separates different cultivars uses starch gel electrophoresis of the gliadin proteins of the endosperm.

Field characters. Habit of growth, leaf size and colour, straw length and wall thickness.

QUALITY IN WHEAT

Although one may speak of a sample of wheat as being of good or bad quality according to whether it is well or badly harvested, plump or shrivelled, clean or mouldy, the term ‘quality’ denotes particularly the suitability of a given variety, at its best, for the purpose for which it is to be used. Since the main use of wheat is for milling and baking, quality normally means suitability for these two purposes.

Milling quality. The primitive methods of reducing wheat grains to flour involved rubbing them between suitably textured stones, using at first saddle querns with to and fro movement of the smaller upper

stone, and at a later period hand driven rotary querns. These gave way later to water and wind mills, with large flat circular millstones, the upper revolving with the grain being fed in around the axle and the flour discharged at the periphery. All these methods ground up the whole grain and gave a brown flour, particularly dark where red-grained wheat was being used; some bran (pericarp and testa) came off in flakes which could be sieved out, but this was the only separation possible. It came to be thought that a whiter flour was superior, perhaps because the use of rye or other substitutes for wheat resulted in even darker coloured bread. By the early nineteenth century a technique of 'high milling' had been developed, using first widely set stones to remove the bran only, followed by normal milling, and so giving a whiter flour. This led to modern methods of milling between steel rollers; here milling is a gradual process involving several passes between fluted break rolls and repeated passes between smooth reduction rolls with intervening screening out of fine fragments. The effect is to give almost complete separation of bran and germ (embryo) from the endosperm which is ground first to coarse fragments (semolina) and then to flour. This flour derived wholly from endosperm is white; it is of lower nutritional value than wholemeal since much of the vitamin and mineral content is removed as well as the fibre, but keeps better in that the readily hydrolysed oil of the embryo is removed.

The speed and efficiency of the process is affected by the quality of the wheat used, and although this is affected by growing conditions and a poor shrivelled sample of very low specific weight will give a low output of flour, it is primarily controlled by the genetic character of the wheat, that is by the cultivar used. The final flour normally passes through a screen with one hundred meshes to the inch, that is the maximum flour particle size is 150–200 μm. This is of the same order of size as the individual starch-parenchyma cells of the endosperm. In a good milling wheat, described as hard, since the endosperm is hard in texture and translucent in appearance when cut, the individual cells separate readily. The resultant flour particles thus consist largely of whole cells, rounded in outline, with only some 20% in the form of particles of under 40 μm, and passing readily through the screens so that the rate of throughput is high. Separation from the bran is also clear-cut, and the percentage of total grain appearing as bran is low (about 12–14%).

Soft wheats are softer in texture, more opaque, appearing chalky when cut, and in them separation occurs largely through rather than between cells. Flour particles are thus irregular in shape, consisting of parts of several cells, with up to 45% in the form of particles under 40

μm, and the flour tends to clog the screens, resulting in a lower rate of throughput. In addition, separation from the bran is less complete and more endosperm is lost with the bran fraction, which may be up to 19–20% of the original grain weight.

Since there is virtually complete removal of the testa in the form of bran, the colour of the flour is not affected by the original grain colour. Different cultivars do however show some slight differences in endosperm colour, which is reflected in the flour; bleaching agents are sometimes employed to improve whiteness. There is a statutory requirement in Britain that white flour shall be fortified, that is that calcium carbonate, iron and vitamin B shall be added in prescribed quantity to compensate for the nutritional loss resulting from the removal of bran and germ.

Baking quality. Bread is essentially a foam of denatured protein, in which are suspended the partially gelatinized starch grains and the other components of the original endosperm cells. Wheat is the only cereal in which the endosperm proteins are such as to produce a suitable persistent foam. Even within the bread wheat species there is considerable variation in the quantity and quality of the proteins, and although it is possible with small-scale baking to make bread from almost any cultivar, for commercial production of acceptable bread it is necessary to use those that give a strong flour. Strength is the ability of the flour to produce a yeasted dough capable of retaining the carbon-dioxide bubbles until the proteins of the bubble walls are denatured and become relatively rigid at about 75°C. The carbon dioxide is produced by the yeast fermenting soluble carbohydrates present in the dough, or produced by the action of amylase on starch. The important proteins are ones not soluble in 10% salt solution; they are collectively known as gluten, and have long-chain molecules with relatively few cross linkings and are thus capable of forming strong films around the bubbles. The strength of the films is increased by repeated stretching; in the older long process methods of making bread this was achieved by allowing the dough to rise, knocking it back and repeating several times before the final baking. In the commonly used short (Chorleywood) process the stretching and consequent rearrangement of the protein chains is achieved by mechanical working followed by a single rise only.

A strong flour results in the production of a loaf of large volume and satisfactory texture; with a weak flour some of the expanding carbon-dioxide escapes before the bubble walls stiffen, and the loaf is of small volume and 'sad' texture. A further advantage to the baker of using strong flour is that more water can be added without spoiling

the consistency of the dough. Thus a strong flour with 13 to 15% protein would allow of 16 gallons of water per sack, to give dough with an extensiometer reading (a measure of mechanical strength) of 800–900 and yield a two-pound loaf with a volume of some 2 800cc, whereas for a weak flour the figures might be 12% protein, 13 or 14 gallons of water, extensiometer reading 450 and loaf volume 2 000cc or less.

Strength of a wheat is mainly genetically controlled, but it is also affected by growing conditions. During this century the bulk of the strong wheat marketed has come from North America and a continental climate appears to favour strength. Genetically strong wheats can however be grown in Britain and suitable cultivars have been available since 1916. They are however lower yielding than the best soft wheats and are therefore only attractive to the grower if their produce commands a higher price. The Home Grown Cereals Authority classification accepts specified strong wheat cultivars as eligible for a price premium. The extent to which a large-scale change to such cultivars is desirable is probably open to debate; it would result in a lower total yield of home grown wheat, and since some 40% of the British wheat requirement during the 1970s has been imported, might well result in increased imports being necessary.

Strength is not purely a function of protein percentage; it is also much affected by gluten quality, and a genetically weak wheat produces a smaller loaf than a strong one at all protein levels. Nevertheless, some increase in strength is possible by increasing the protein content of the endosperm by late nitrogenous manuring, although only with genetically strong cultivars is there a consistent improvement. A further potential method of obtaining stronger flour from genetically weak wheats is the use of air classification milling. If flour is reground the finer particles consist largely of the protein matrix from between the starch grains, rather than of all the cell constituents, and some 20% of the original mass of the flour can be removed as fine flour of under 17 μm with a protein content of 18%.

In practice however the main factors affecting the use of relatively weak wheats for bread are baking techniques. The Chorleywood process, by mechanical increase of dough strength, enables a larger proportion of weak flour to be used in the mix without reduction in loaf volume. Chemical 'improvers' are widely used; these are substances such as potassium bromate, ascorbic acid and chlorine dioxide (this last also acts as a bleaching agent) which have the effect of increasing the mechanical strength of the protein films.

An additional factor affecting the value of wheat for bread making is the alpha-amylase content. This enzyme is responsible for the

breakdown of starch to sugar which can be fermented by yeast, and to this extent is desirable. The alpha-amylase of wheat is however heat stable, and if present in large amounts may continue to act on starch during the early stages of baking, causing a deterioration of crumb structure. Wheat which has begun to sprout may have a very high enzyme content and be quite unusable, but some cultivars have an excessive alpha-amylase content even in a perfect sample, and for this reason are undesirable for bread making. Wheats with very low amylase can be used, since it is possible to add yeast nutrients directly to the dough mix, or alternatively to include extra amylase of fungal origin, which is readily inactivated by heat, and therefore harmless.

For biscuit making the requirements are different; the dough is not required to rise, and a weak flour is needed. The difficulty here is that there is a fairly close connection between strength and hardness, and that all weak wheats are also rather soft. However, a number of cultivars of passable milling quality and good biscuit-making quality are available.

BREAD WHEAT CULTIVARS IN BRITAIN

The combined requirements of the farmer for high-yielding, strong-standing, disease-resistant varieties and of the miller and baker for high quality present a very difficult problem for the plant-breeder. It has been met by the successive crossing of varieties, each with their particular merits, derived from almost all over the world, in an endeavour to produce new varieties combining as many as possible of the qualities required. Outstanding work has been done in Britain at Cambridge, and by individual firms, and at the same time there has been a constant introduction of varieties developed in other countries with sufficiently similar climatic conditions. Field experience, and the systematic trials undertaken by the N.I.A.B., have acted as a sieve, sorting out and retaining the best varieties and rejecting the inferior ones, whether old and formerly valuable varieties now superseded, or new introductions of insufficient merit. Few of the older varieties remain in cultivation, and the 'life' of the majority of varieties is short. Thus, of the twenty wheats in the 1955 revision of the N.I.A.B. lists of recommended wheat varieties, only six were included in the recommended list for 1960, and of these six, only two were still recommended in 1965; similarly, of the twenty-two cultivars in the 1977 list, only three date from before 1970. For information on the present cultivars the current list should be consulted; it is here only possible to survey the past changes and the trends observable.

Wheat yields in Britain had increased from some ten bushels per

acre, say 700 kg/ha, in the fourteenth century to about twenty bushels, 1 400 kg/ha, in the seventeenth century and about 30 bushels, say two tonnes/ha, by the beginning of the twentieth century. Some of the countries in north-western Europe had slightly higher yields, but the world average was probably under one tonne/ha. There is little detailed information available on cultivars used in earlier times; at the beginning of this century the winter wheats used in Britain were of the Squarehead type, rather weak wheats, long strawed by modern standards but then amongst the best-standing wheats available; one of these, Squarehead's Master, first recorded in the 1880s, remained in occasional use as a special purpose wheat until 1960. Crosses between these Squareheads and similar wheats in Holland gave Victor (introduced 1908 and recommended up to 1957), Juliana (recommended 1936–57) and other similar white-grained biscuit wheats. Wheat strong enough to be used for the large-scale baking which had by then become important was being imported at the beginning of the century from North America, and included the cultivar Red Fife, a very hard strong but low-yielding spring wheat derived from an importation from Poland. Professor Biffen at Cambridge showed that the strength of Red Fife was genetic, and was retained when it was grown in Britain. The yield of Red Fife here was far too low for it to be economic, but Biffen, by crossing it with a Squarehead, produced in 1916 the winter wheat Yeoman (recommended up to 1957); this was the first strong wheat giving reasonably high yields in Britain. Holdfast (1936–58) was a white wheat of rather similar origin, and from this, by crosses with higher yielding French wheats were derived Maris Widgeon (1964–77) and later Maris Freeman (1974–) which retained the strength of the Fife ancestor, combined with much higher yield. The French winter wheats, large-grained, stiff standing forms with semi-solid straw, better adapted to high levels of nitrogenous manuring than the older British wheats, were introduced during the 1930s. Although most were of relatively low quality, they rapidly became popular on account of their high yield. Among them may be mentioned Bersee (1935–59), and at a later period its strong derivatives Elite Lepeuple (1960–70) and Flinor (1974–), and also Hybrid 46 (1953–70) and particularly Cappelle Desprez (1953–76). This latter cultivar was outstanding; not only did it remain on the Recommended List for twenty-four years, at a time when most cultivars were surviving for a few years only, but it came to occupy at its peak in the mid–1960s some 80% of the British winter wheat area, and was so widely and so successfully used by plant breeders as a parent that in 1976, the last year in which Cappelle Desprez itself was recommended, ten out of

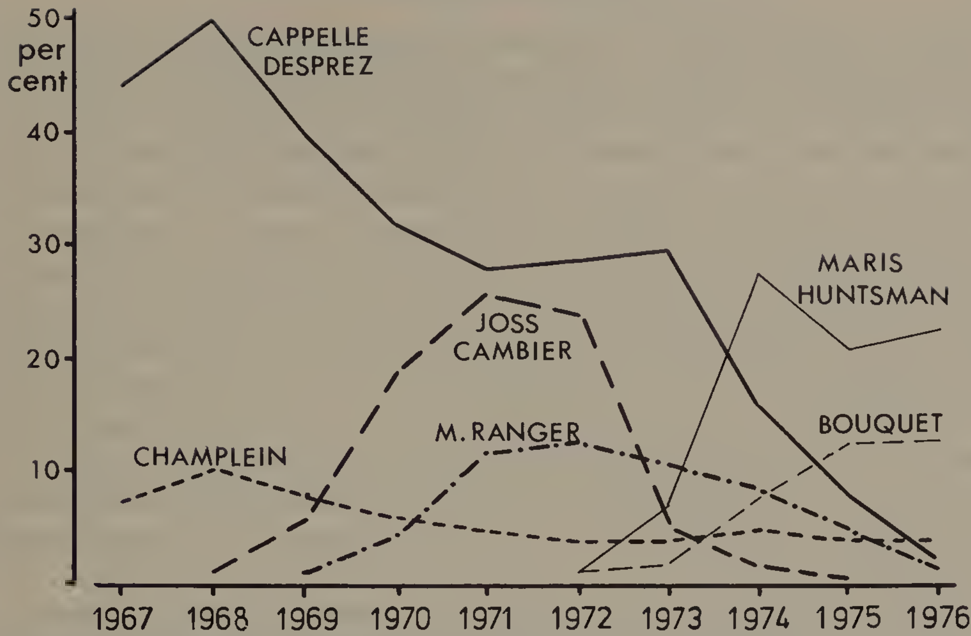


Fig. 22. Changes in popularity of selected winter wheat cultivars over a ten year period. The figures are for numbers of samples of the particular cultivar submitted to the Official Seed Testing Station expressed as a percentage of the total wheat samples submitted during the year. In the absence of any direct statistics of cultivar use, this gives a useful measure of relative popularity. In the period covered Cappelle Desprez shows a slow decline from its earlier peak; it is succeeded by Joss Cambier and Maris Ranger, and these in turn by Maris Huntsman and Bouquet. Data from N.I.A.B. *Annual Reports.*

the other fifteen recommended winter cultivars were Cappelle Desprez derivatives. Professeur Marchal (1960–6) with a complex pedigree involving British, Swedish and French wheats and Red Fife derivatives, was used in the breeding of Maris Nimrod (1971–7), Maris Huntsman (1972–) and Kinsman (1976–). All of these unfortunately inherited from Professeur Marchal some tendency to high alpha-amylase activity, but from the grower's point of view this was compensated for by their high yield, and Maris Huntsman in particular achieved some 28% of the wheat area by 1974.

Spring wheats in the early part of the century were either old British forms such as April Bearded, or not very satisfactory French spring varieties. The introduction of Atle (1939–65) and other similar forms altered the position, and made spring wheat, for the first time, a satisfactory alternative to winter wheat. Atle was derived from the Swedish Kolben, which had in fact originated in the same area in Poland as Red Fife, which it resembled in strength, and to which it was probably related. Crosses of Kolben and Fife derivatives with various German wheats gave Koga II (1957–70), weaker but higher yielding, and from that were derived the more recent spring

cultivars Kolibri (1968–75), Kleiber (1971–77), Maris Dove (1971–) and Maris Butler (1973–). Kolben derivatives were also involved in the production of Maris Ranger (1968–) from which were derived Maris Freeman and Kinsman, already mentioned; all these are classed as winter wheats, but have very low vernalization requirements.

A new departure during the 1970s, which may be important in British wheat improvement, is the introduction of a particular form of dwarfing, derived from Mexican dwarf wheats, which have already played a conspicuous part in the improvement of wheat in many agriculturally less developed areas. This dwarfing was derived from Norin 10, of Japanese origin, and is due, not as in many dwarf plants, to a shortage of gibberellic acid, but to a blockage in its physiological use. Such dwarfs are highly efficient photosynthetically; Hobbit (1977–) is an example of a semi-dwarf cultivar of this type.

During the three-quarters of a century covered by this brief review wheat yields in Britain have approximately doubled. This increase has been achieved by a combination of improved growing techniques and the breeding of improved varieties. More intensive growing methods, with higher inputs of nitrogen and of fungicides, and careful control of plant population and possibly, by the use of cycocel, of straw length, may perhaps lead to higher and more consistent yields. The plant breeding story has been essentially the development of progressively higher yielding, shorter strawed, stiffer standing cultivars (and, to a more limited extent, ones of higher quality), mainly by the intercrossing of the best commercial varieties available at the time.

By itself, however, this is not enough; a potentially high yielding cultivar, however good it may be when healthy, is of little value if it is commonly attacked by damaging diseases. Chemical control of many wheat diseases is either expensive or ineffective, and a satisfactory wheat cultivar therefore needs genetic resistance to disease. In some cases resistance was available in existing commercial cultivars; Capelle Desprez for instance owed some of its popularity to the fact that it was, at the time of its introduction, one of the few cultivars with at least fair genetic resistance to eyespot, inherited from its parent Hybride du Jonquois, and passed on to many of its descendants. In other cases however suitable resistance genes could only be found in obscure varieties or in other species, and consequently the pedigrees of many modern cultivars include for example *Triticum carthlicum*, *T. durum* or *T. timopheevi* as sources of mildew resistance, or of *Aegilops* species or old and low yielding bread wheat cultivars as sources of resistance to yellow rust. The wheat breeder's task is still

further complicated by the fact that many of these sources supply only race-specific ('vertical') resistance genes, and that the resistance they confer is not permanent. Many cultivars have been introduced which have gone through their trial period successfully, because they were resistant to the races of fungi then present, only to fail in a later year when they came in contact with a newly mutated or freshly introduced race of the fungus, to which they were susceptible. Permanent non-race-specific ('horizontal') resistance would of course be preferable, but this is usually very incomplete, difficult to find and assess, and dependent on numerous genes and therefore difficult for the breeder to work with.

The list of diseases which the wheat breeder needs to take into account is a long one: yellow and brown rusts (black rust, although a major preoccupation of breeders in many warmer areas is too rare in Britain to be important), mildew, eyespot, loose smut (bunt is cheaply and effectively controlled by seed dressing), glume blotch, and, among physiological 'diseases', manganese deficiency. To this list may eventually be added take-all; so far no source of genetic resistance to this is known, but there is some slight genetic variation in susceptibility, and resistance genes may one day be available.

Hybrid wheat

A development which might affect the whole future course of breeding would be the production of hybrid wheat. Existing cultivars are of course self-pollinating, and no advantage can be taken of heterosis; in fact in normal wheat breeding care is taken to avoid selection, in the first few generations after an initial cross, for hybrid vigour effects which will disappear in later generations. In F.1 hybrids an increase due to heterosis of up to 30% in yield is perhaps possible. A male-sterile parent would be needed for any large scale production of hybrids; this could be obtained using *Triticum aestivum* nuclei in *T. timopheevi* cytoplasm, and fertility restorer genes are available. It would of course still be necessary to breed for all the required characters, and to maintain the two parent lines. The practical difficulties, including that of ensuring adequate pollination, are very considerable, and the cost of the hybrid seed would necessarily be high, but the success that has been achieved with the cereals maize and sorghum, and with an increasing number of other crops, has led to very determined efforts to develop hybrid wheat, and these may ultimately be successful.

RYE

Rye belongs to the genus *Secale*; this is closely related to *Triticum*, and has a very similar spike, but with much smaller, narrow glumes.

Secale cereale L. **Cultivated Rye**

The only species cultivated. This is an annual with rather lax spikes of usually three-flowered spikelets; the third flower is nearly always abortive and minute. The glumes are narrow and acute, the lemmas longer than the glumes, tapering gradually into long, rather stout awns, and bearing stiff hairs on the keel. The lemma and palea of each floret tend to diverge, so that the tip of the mature caryopsis is clearly visible. The caryopsis, which threshes out in all cultivated forms of rye, is similar in structure to that of wheat, but considerably longer and more slender.

Germination is similar to that of wheat, but usually only three lateral seminal roots are produced. The young plant closely resembles wheat, but the coleoptile and leaves tend to show a purplish

Fig. 23. Rye. A, spike in side view, ×½. B, single spikelet and separate parts, ×3. G, glumes. L, lemma. P, palea. C, caryopsis (shown in dorsal and ventral views and cross-section). R, rachis.

tint, and the auricles are small, very narrow and hairless. The straw is long, slender, solid and wiry.

Origin. Cultivated rye appears to have been derived from *S. montanum* Guss. or a related species. This is a wild plant of E. Europe and W. Asia, similar to cultivated rye and, like it, a diploid with fourteen chromosomes. It differs in being perennial, in having smaller grains and a brittle rachis. Annual and biennial forms with brittle rachis such as *S. ancestrale* Zuk. and *S. segetale* Zuk. occur as weeds of other cereals in south-western Asia, and these appear to be the primitive forms of *S. cereale.* Rye has never been cultivated in the area in which these wild forms occur, and it appears probable, therefore, that they were carried westwards and northwards into central Europe quite unintentionally as weeds of wheat. As the mixed crop was taken north, conditions became less and less favourable for the wheat, so that the crops harvested contained ever-increasing proportions of rye, which in primitive agricultural conditions could not, of course, be cleaned out. Ultimately, in central and northern Europe, the non-hardy Mediterranean wheat would disappear entirely, and the rye remain as a secondary or replacing crop. The first archaeological finds of rye as a crop date to the first millenium B.C.; it was widespread in central Europe in Roman times, but not found in Britain in any quantity until the Middle Ages.

Cultivars

Rye differs very conspicuously from wheat in being largely cross-pollinated; individual plants therefore tend to be mainly heterozygous, and cultivars are much less uniform and well-marked than in wheat. This fact, together with its minor importance in Britain, meant that little attention was paid to variety in rye, and it was often sold and grown merely as 'winter rye'. Winter and spring forms differ in the same way as in wheat; the lower yielding spring rye is never grown in Britain. Winter rye is grown both as a cereal for grain production and as a herbage plant for spring grazing; different cultivars are used for these two purposes.

For grain, the old very long strawed form has been replaced by newer cultivars, somewhat shorter strawed and higher yielding; they include Dominant and Ashill Pearl. Autotetraploid cultivars of rye, as for instance Tetra Gorzow, have been produced; they have twenty-eight chromosomes, and show some promise of increased grain size and yield. Their use is, however, complicated by the necessity for isolation from normal diploid rye, since cross-

pollination with pollen of different chromosome number will result in sterility and loss of yield.

Uses of grain

Rye can be used for bread making, but the bread is generally regarded as inferior to that made from wheat, and rye is used as a main bread corn only where conditions are unsuitable for wheat growing. It behaves on milling like a soft wheat; for bread a low extraction rate of about 65% is used, since higher extraction rates give very dark and strong flavoured bread. In baking the dough is very weak, since the proteins present are not true gluten, and this is only partially compensated for by the more abundant pentosans. The chemical 'improvers' used to increase the strength of wheat dough are not effective with rye, and the addition of strong wheat flour is the only practicable method of producing a stronger dough. Rye is grown in Britain for grain only on contract for the production of proprietary rye biscuits, made from wholemeal flour, and in North America mainly for whiskey. The thin hard straw is of little value for animal feeding, and is used for litter, thatching or packing.

The only advantage of rye over wheat is its greater hardiness, and its ability to yield satisfactorily on somewhat acid soils of low fertility. There is thus always a tendency, with greater efficiency of farming and rising standards of living, for rye to be replaced by wheat. It was formerly an important bread corn in Britain, but its use for this purpose is now largely confined to East Germany, Poland and Russia.

Use for forage

Rye has been used as a constituent of various arable silage mixtures, but a more important use is for spring grazing. Sown in September it is sufficiently winter hardy and quick growing at low temperatures to produce leafy vegetative material to provide grazing in March, before Italian ryegrass has much growth. Normally it is used purely as a temporary crop and ploughed up after grazing; special cultivars, long strawed and low yielding if grown for grain, are used, including the British Greenfold and Rheidol, and the Hungarian Lovaszpatonai.

TRITICALE

Rye is sufficiently closely related to wheat for crosses to be possible, and indeed a number of bread wheat cultivars have been produced which contain small amounts of genetic material from rye. Rye

chromosomes do not however pair normally with any of the wheat chromosomes at meiosis, so that for instance in a cross between bread wheat and rye, with normal reduced gametes, the tetraploid progeny with twenty-eight chromosomes ABDR is sterile. If chromosome doubling takes place to produce the octoploid AABBDDRR this is fertile, and behaves as a new species. Such fertile allopolyploid *Triticum* × *Secale* hybrids are named Triticale. This is often used as both common and proper name, but the alternative proper name × *Triticosecale* is sometimes preferred.

Such Triticale forms, which are intermediate in structure between the two parents but usually more closely resembling wheat, have been known for the greater part of this century. The earlier hybrids were disappointing, and the hope of producing immediately a crop with the quality of wheat and the hardiness of rye was not realized. Continued work and selection has much improved the results, and by the 1970s Triticale forms have reached the stage of commercial crops in Canada and eastern Europe, and are potentially of value in Britain. Results are conflicting, as would be expected in view of the wide range of parent forms which have been employed. In general the hexaploid forms AABBRR, mainly durum wheat × rye, appear to be more satisfactory than the octoploids. The better forms are often hexaploid derivatives of crosses of these with bread wheat, in which the RR genome has been modified by the incorporation of material from the DD chromosomes of the wheat. In the best forms yields approaching those of wheat have been obtained, with higher protein contents. Some of the earlier produced Triticale forms showed reduced fertility and very marked susceptibility to the fungal disease ergot, which results in the caryopsis being replaced by a poisonous sclerotium, but the more recent forms are free from this defect. Triticale forms also show promise for whole-plant forage, with protein and soluble carbohydrate contents exceeding those of wheat or rye.

BARLEY

Barley belongs to the genus *Hordeum*. The inflorescence, like that of wheat, which is placed in the same tribe of the *Gramineae*, is a spike. The arrangement of the spikelets is, however, quite different from that seen in wheat; in barley each node of the rachis bears three single-flowered spikelets.

Hordeum sativum Jess.* **Cultivated Barley**

This is an annual with large spikes; each node of the rachis bears

* Other names are also in use, see p. 89.

three spikelets, each consisting of a pair of small linear glumes, and a single floret with a lemma larger than the glumes, partly enclosing the palea. The rachilla is prolonged above the base of the floret. The rachis is tough in the cultivated barleys and the caryopsis either threshes out (naked or hull-less barleys, not grown in Britain) (Fig. 29) or threshes off the rachis enclosed within the lemma and palea which not only tightly enwrap it, but are stuck to it by a secretion produced by the pericarp.

The caryopsis differs from that of wheat in minor details only; it is more pointed at the apex, and the aleurone layer consists of several layers of cells instead of one. In the 'hulled' barleys grown in Britain, the caryopsis is completely hidden by the lemma and palea; the five-nerved lemma extends some two-thirds of the way round, its margins overlapping those of the palea. The palea shows a ventral groove corresponding to that of the caryopsis; in the lower part of the groove lies the slender rachilla. Within the base of the lemma, and between it and the embryo region of the caryopsis, is the pair of lodicules, which may be large or small.

Germination is similar to that of wheat, but the coleoptile, in the hulled barleys, grows up inside the lemma and therefore appears to emerge from the apex of the grain. Seminal roots may be up to eight in number. The young plant is distinguished from wheat by its much larger auricles and usually by its glabrous leaf-sheaths; in some winter barleys hairs are present, but not on the auricles themselves. The leaf blades show usually some fifteen to twenty nerves as against eleven to thirteen in wheat; as in wheat, the leaf blades tend to be twisted in a clockwise spiral. The life-history of barley also resembles that of wheat, and the same distinction into winter and spring forms exists. Like wheat again, cultivated barley is self-pollinated, the florets of the large-lodiculed forms usually opening for a short period after anther dehiscence, those of the small-lodiculed forms remaining closed throughout. Growth is in general similar to that of wheat, but a larger proportion, some 30%, of the grain yield comes from the photosynthesis of the ear itself. This is perhaps associated with the presence of the large awns; awnless forms exist but are rarely used, and never in Britain.

Range of types

If all three spikelets of each node produce a grain, six vertical lines of grains will be visible on the ear. If the internodes of the rachis are short—that is, if the ear is dense, these vertical lines will be spread equidistantly around the rachis, giving a typical *six-rowed barley*. If,

Fig. 24. Barley spikes. A, dense six-row. B, lax six-row (i.e. four-row). C, dense two-row. D, lax two-row. (A and B in face view, C and D in side view.) $\times\frac{1}{2}$.

however, the ear is lax, the lateral two spikelets at each node have room to stand more nearly opposite to each other, and hence come almost in a vertical line with those of the node above, giving the so-called *four-rowed barleys*, in which there are two single vertical rows, formed by the grains of the central spikelets, and two double rows formed by those of the lateral spikelets. In many barleys, however, the lateral spikelets are much smaller than the central one at each node, and do not produce a grain, so that a *two-rowed barley* is produced.

Four- and six-rowed are distinguished only by difference of density, and grade one into the other. The distinction from two-rowed forms is, however, quite clear-cut (intermediate types, in which the lateral spikelets are fertile but smaller than the central ones do occur, but are of no economic importance) and the appearance of the ear is very distinct. Samples of threshed grain can also be distinguished; in two-rowed barleys all the grains are symmetrical but in four- or six-rowed forms the lateral grains are asymmetrical and slightly twisted, and the sample thus consists of one-third straight grains and two-thirds twisted grains.

Differences of ear density are also shown in the two-rowed barleys;

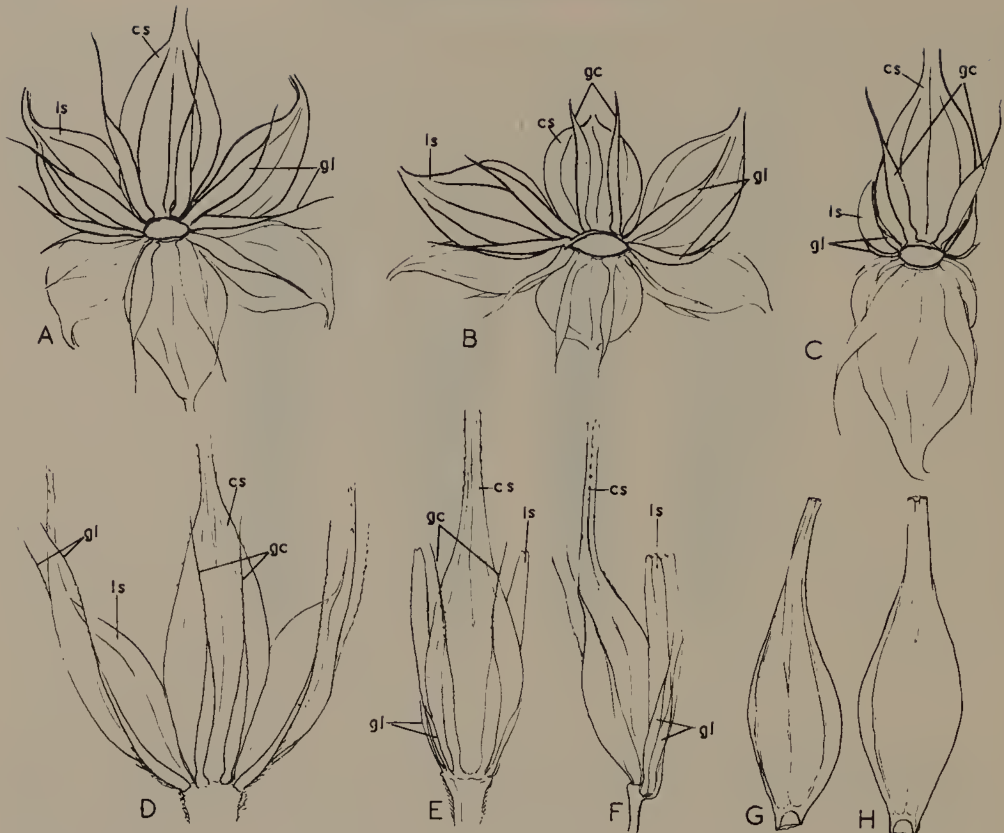


Fig. 25. Barley. A, B, C, part of spike seen from below, to show arrangement of fertile spikelets at two successive nodes to form A, six rows; B, four rows; C, two rows. D, E, F, group of three spikelets at one node; D, of a four-row barley in face view; E, of a two-row barley in face view; F, in side view. G, H, dorsal view of threshed grains of a four-row barley; G, a lateral grain; H, a central grain. All ×3. *cs,* single floret of central spikelet. *ls,* of a lateral spikelet. *gc,* glumes of central spikelet. *gl,* of lateral spikelet.

where the ear is lax and the internodes of the rachis long, the grains make only a small angle with the rachis, giving a *narrow-eared barley*. Where the ear is dense, the grains stand out more nearly horizontally, making a larger angle with the rachis and giving a *broad-eared barley*. Within each of these groups various degrees of density occur.

The base of the mature grain varies in shape. It may be square as seen in side view, often with a shallow, transverse 'nick' across the base of the lemma about 1 mm from the point of attachment (*verum type*); or it may be bevelled off to a blunt, chisel-like edge (*falsum type*). The lodicule characters are correlated with those of the grain-base; varieties with *verum*-type base have small lodicules lying wholly on top of the caryopsis, as seen when the lower part of the lemma is dissected off. Varieties with *falsum*-type bevelled grain-base have larger lodicules, partially hidden in the dissected grain by the base of the caryopsis, and with their tips curving round it in a collar-like

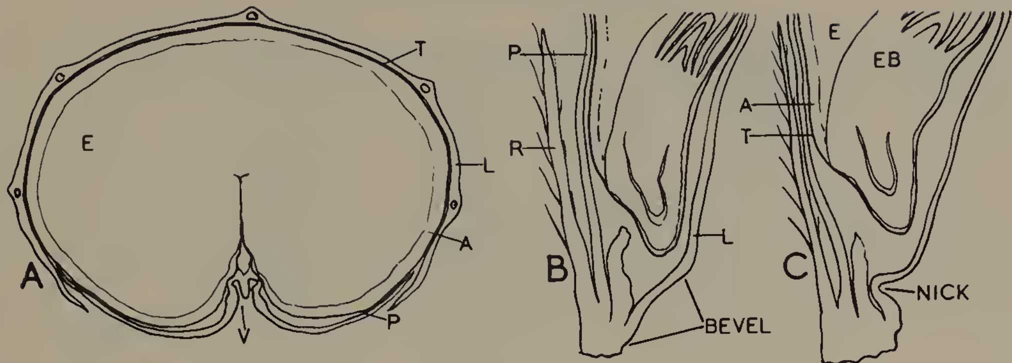


Fig. 26. A, diagrammatic transverse section of mature barley grain. B, diagrammatic median vertical section through lower part of grain with *falsum* type base. C, with *verum* type. All ×12. R, rachilla. L, lemma. P, palea. T, pericarp and testa. A, aleurone layer. E, endosperm. EB, embryo. V, ventral groove.

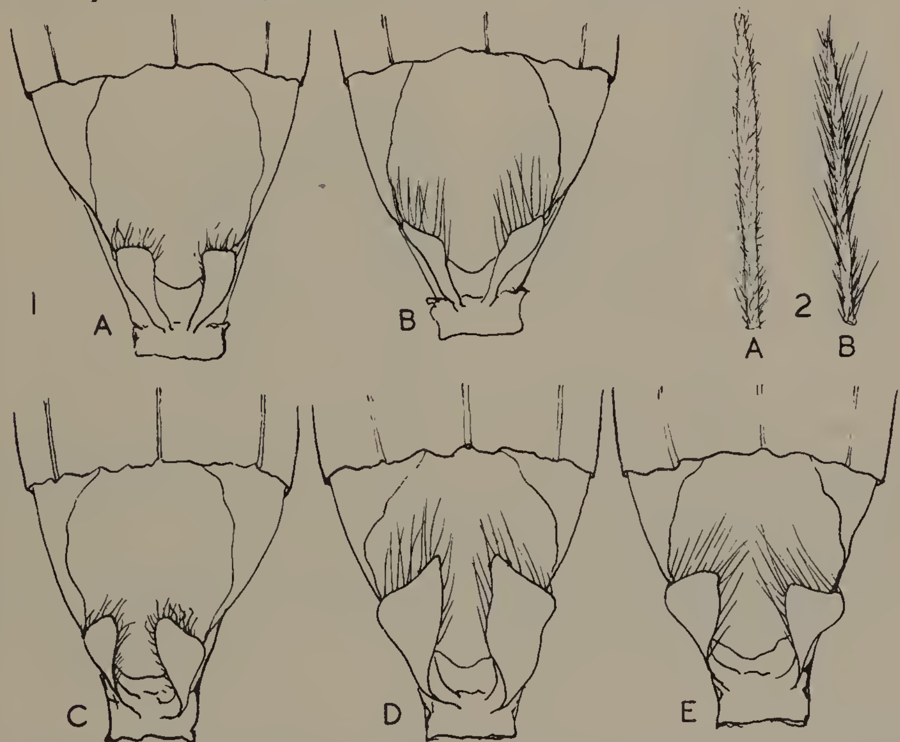


Fig. 27. 1, barley grains with basal part of lemma dissected off to expose lodicules and embryo region of caryopsis; A, lodicules small (bib-type), hairs woolly (Maltster); B, lodicules small, hairs straight (Plumage Archer); C, lodicules large (collar-type), hairs woolly (Chevallier); D, lodicules large, pointed, hairs straight (Spratt-Archer); E, as D, but lodicules blunt (Kenia). 2, detached rachilla: A, with woolly hairs (Chevallier type); B, with straight hairs (Archer type). All ×9.

fashion. Hairs are present on the lodicules and also on the rachilla, and the type of hair found is the same on both; these may be either long and fairly straight (Archer type, conveniently called 'hairy') or short and curved (Chevallier type, 'woolly'). Type of hair is not correlated with grain-base, and each of the two rachilla and lodicule

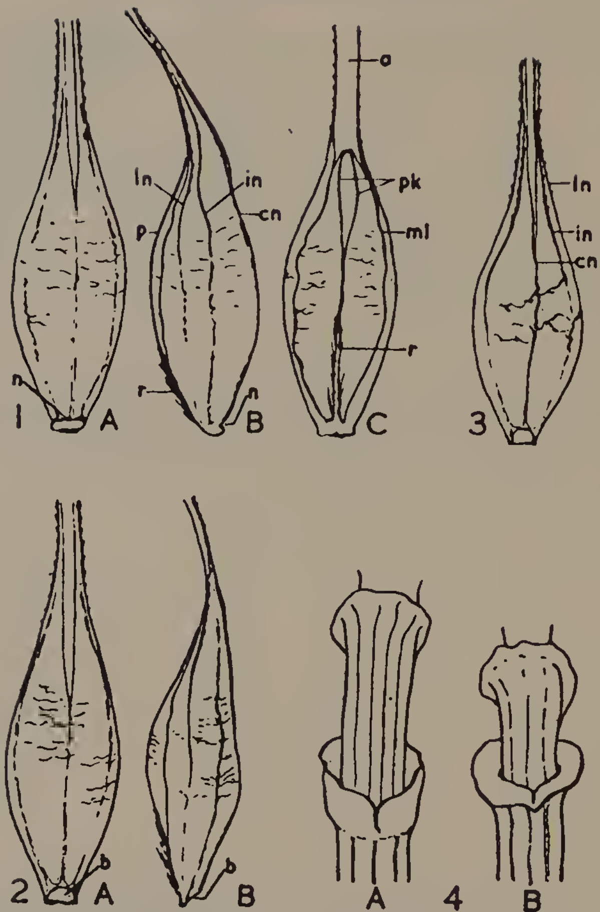


Fig. 28. Barley. 1, grains of Plumage-Archer (two-rowed, dense, *verum* base): in A, dorsal; B, side view; C, ventral view. 2, Spratt-Archer (two-rowed, lax, *falsum* base, English type); A, dorsal view; B, side view. 3, Freja (as 2, but continental type), dorsal view. All ×3. 4, collar at base of lowest internode of spike: A, Spratt-Archer (cup type); B, Freja (plate or platform type); ×7. *a,* awn. *b,* bevel. *n,* nick. *p,* palea. *pk,* the two keels of palea. *r,* rachilla. *cn, in, ln,* central, intermediate and lateral nerves of lemma. *ml,* margin of lemma.

hair types may be found associated with either *verum* or *falsum* grain-base.

Type of grain-base is not necessarily correlated with density, but in fact all the narrow-eared two-rowed barley varieties grown in Britain show the bevelled *falsum* base, while all the broad-eared forms, with the exception of the long obsolete Spratt, have *verum* base.

Cultivar distinction

The majority of barley cultivars used in Britain, whether two- or six-rowed, are lax or medium-lax types with *falsum* grain-base and straight hairs. It is therefore necessary to use a number of other minor characters to distinguish between them. These include:

Ear. Shape and length; length of awns, shape and angle of lateral spikelets in two-rowed forms. Shape and hairiness of rachis segments. Shape of collar at base of spike: platform or cup type, horizontal or oblique.

Grain. Size, wrinkling, presence of anthocyanin along nerves of lemma and in aleurone layer, length of rachilla and of rachilla hairs, presence or absence of hairs in ventral groove, presence or absence of teeth (spicules) on intermediate nerves of lemma, or between nerves.

Field characters. Differences in growth habit and leaf attitude, length of neck and attitude of mature ear. Susceptibility or resistance to damage by DDT.

Nomenclature

All the forms of cultivated barley will cross with one another, and many of the distinctions between them are single gene differences. It seems desirable therefore to regard them as belonging to a single species, and *Hordeum sativum* Jess., which is used here, is the earliest name used in this sense. The main forms had however previously been named as separate species, *H. polystichum* L. six-rowed barley, and *H. distichum* L. two-rowed barley; the O.E.E.C. classification retains this distinction and uses these two specific names. The British Plant Breeders' Rights classification, however, uses the name '*H. vulgare* sensu lato' (i.e. 'in the broad sense') to cover all the cultivated barleys; *H. vulgare* L. in the strict sense appears to have applied only to the four-rowed, that is to the lax six-rowed barleys, the dense six-rowed forms being named *H. hexastichum* L. Other names which have been used, either as specific or subspecific epithets, are *zeocriton* for the very broad two-rowed fan barley Spratt, *erectum* for the dense broad eared and *nutans* for the lax narrow-eared two-rowed barleys. *H. deficiens* Steud. refers to extreme two-rowed forms with lateral spikelets minute or absent and *H. trifurcatum* Jacq. to the awnless forms with hooded lemma, whether two- or six-rowed, known as Himalayan or Nepal barley.

Origin and history of cultivated barley

The wild barley species *Hordeum spontaneum* L. occurs in much the same region and in the same conditions as the wild wheats, extending from Syria south of the Caspian to Turkestan. Like the wild wheats it has a very fragile rachis and a large self-burying diaspore; this consists of a single sharp-pointed length of rachis, to which are attached the

central rather narrow large-awned fertile spikelets, and, standing at a slight angle to this and acting as barbs, the smaller shortly-stalked awned lateral male spikelets. It is thus functionally a two-rowed barley, although the lateral spikelets are larger and more strongly awned than in the cultivated two-rowed forms. It sometimes occurs in mixed stands with the wild wheats, and appears like them to have been exploited by the Natufians and brought into cultivation at about the same time as the wheats. Cultivation resulted in the same sort of changes as in the wheats, with loss of extreme fragility and self-burying characters, and thus gave rise to cultivated two-rowed barleys; transitional forms with some of the wild features have been recorded from Jarmo, dating to the beginning of the seventh millenium B.C. At about the same time, or perhaps even earlier, six-rowed forms are recorded, some hulled, some naked. It is assumed that these arose by mutation at an early stage of cultivation. Dense and lax six-rowed forms appear to have developed at about the same time, perhaps independently; dense forms are found mainly in hilly areas, lax in the lowlands. The main spread of barley cultivation appears to have been of six-rowed forms, which in some cases replaced two-rowed cultivated forms in Egypt and south-western Asia in the fifth millenium B.C., and it was six-rowed barley which spread northwards through Europe; two-rowed forms are not recorded in northern Europe until the Middle Ages.

A wild six-rowed barley *H. agriocrithon* Aberg. is known, but it is rare, recorded only as a weed of corn fields and not in any natural habitat. It has been found in Tibet and in a few localities in south-western Asia, and does not appear to be a genuinely wild species; it probably arose as a cross between wild two-rowed and cultivated six-rowed forms. No clearly distinct species are known which will cross with *H. spontaneum* and its derivatives, and interspecific hybridization and polyploidy have played no part in the development of cultivated barleys.

Uses

Barley was formerly used largely as a cereal for human food, and many of the forms cultivated were naked barleys, in which the caryopsis alone threshes out. Such naked barleys (mainly six-rowed, but two-rowed forms exist) are still cultivated in areas in Asia unsuited to wheat-growing; in regions such as Britain, where barley is now used either for stock-feeding or for malting, only hulled forms, in which the caryopsis remains firmly enclosed within the lemma and palea, are used. These may be either two- or six-rowed forms; in

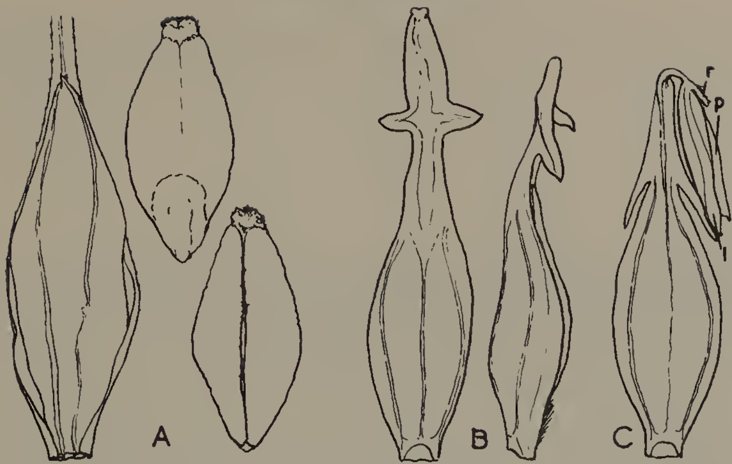


Fig. 29. A, naked barley; ventral view of spikelets to show loosely fitting palea and lemma, threshed caryopsis in dorsal and ventral views. B, hooded (Himalayan) barley grain in dorsal and side views. C, hooded grain in which an extra spikelet has developed on hood. *r, p,* and *l,* rachilla, palea and lemma of extra spikelet. All ×3.

Britain six-rowed forms are used only for feeding, but in the United States, for example, they are the main malting barleys.

In Britain the small quantity of barley used for direct human consumption is prepared by abrading hulled barley to remove the lemma and palea; this 'blocked barley' is further treated to remove most of the bran and germ, giving pearl barley (about 60% of the whole grain). Barley flour is obtained by roller milling pearl barley at about 80% extraction rate, equivalent to some 50% of the whole grain.

For stock feeding most hulled barleys have a satisfactory fibre content, but some of the six-rowed winter cultivars have an excessively thick lemma, and therefore a low digestibility. Barley has been found to be a very satisfactory carbohydrate source for ruminants, but the protein percentage is low, and the protein, like that of many cereals, deficient in the amino-acid lysine. Possible sources of higher lysine and perhaps higher total protein are available to the plant breeder in Hiproly and Risø 1508, and these may give rise to improved cultivars specifically designed for feeding. At present the character of the grain for stock feeding is not regarded as critical, providing the yield is high enough, but for malting purposes grain characters are of very great importance, and quite small differences may have a marked effect on quality and value. In neither case is the character of the awn important, since it is removed in threshing, but where barley is cut green for fodder or hay the rough awn of the common malting and feeding varieties is a distinct disadvantage, and either smooth awned or awnless (hooded) forms are used. Neither of these forms is commonly used for grain, since in both the caryopsis

tends to be only loosely held by the lemma, and the smooth awned character is associated with reduced size of stigma and reduced fertility.

Malting quality

The malting process consists essentially of germination under carefully controlled conditions. The barley grain is soaked (steeped) for two days and then drained, after which germination (modification) is allowed to take place for up to seven days. Gibberellic acid (0·2 parts per million) is often added to speed germination. During this time enzymes are produced by the scutellum and aleurone layer, and the cellular structure of the endosperm is largely broken down. Considerable root growth takes place, and the coleoptile grows up under the lemma; this growth is at the expense of part of the starch originally present. Germination is then stopped by kilning at 80°C for up to five days, and the shrivelled roots and coleoptiles sieved out. The resulting malt then passes to the brewer.

In brewing, the malt is ground and soaked at about 65°C; the starch is broken down to maltose by the amylases produced during malting. The solution (wort) is filtered (high beta-glucan gum content of the barley is undesirable since it may slow filtration), sterilized and boiled with hops; this results in precipitation of the proteins present. The wort is then filtered, cooled and fermented with yeast, using either top yeast *Saccharomyces cerevisiae* (usual for British beers) or bottom yeast *S. carlsburgensis* (most European beers and lagers). The type of beer to be produced affects the details of the malting technique and the type of barley cultivar preferred. Cereals other than barley can be malted, but this is rarely done now.

For the barley to malt satisfactorily it is essential that germination shall be very high, very rapid and very uniform. Dead grains will not merely not malt, but are likely to give rise to undesirable fungal growth; dormant grains will delay the process, and if some grains germinate more rapidly than others, it will be impossible to stop germination at the optimum stage for all grains. The physical state of the endosperm must also be satisfactory; 'steely' grains, which show a semi-translucent surface on cutting, are undesirable, as the endosperm structure breaks down incompletely or more slowly than in a grain showing an opaque, floury cut surface. This necessitates a longer germination period with increased growth of the embryo, and therefore greater loss of carbohydrate from the endosperm. High nitrogen content is undesirable, since it means a lower carbohydrate content; in addition, it gives a higher percentage of nitrogen com-

pounds in the final extract, which is for most brewing purposes a disadvantage.

These characters of the grain, on which the malting value of a sample depends, are determined partly by the variety and partly by the way in which it is grown. Slow ripening and complete maturity are essential for high malting value; quality is decreased by drought or excessive rain, by late sowing, and by late or excessive nitrogenous manuring; it is also very much influenced by soil conditions. Quality can ultimately only be judged by malting and brewing tests, but nitrogen percentage may be a good guide. It varies from about 1·3% in good malting samples to nearly 2% in poor ones, and it has been shown that for any given variety the yield of extract from the malt is decreased by an amount proportionate to any increase in the nitrogen content of the grain. Size of grain, as expressed by weight per 1 000 grains, also affects yield of extract, as smaller grains tend to have a higher proportion of lemma and palea, and therefore a lower starch content. On appearance, a sample is judged by the type of endosperm as seen on cutting, on the absence of threshing damage or moulding, on the size, uniformity and well-filled condition of the grain, and on the clear, pale yellow colour and finely-wrinkled appearance of the lemma and palea. This latter character is due to the thin lemma and palea adhering to the caryopsis during its final slight shrinkage resulting from loss of water after it has reached its full size.

BARLEY CULTIVARS IN BRITAIN

Although barley, mainly six-rowed types, had been widely cultivated in Britain for human food in earlier times, by the nineteenth century most of the barley crop consisted of two-rowed spring forms grown primarily for malting; the hardy six-rowed land-race Bere was used in upland areas for stock feeding. The main malting barleys were land races with very slender arching ears and hairy rachilla. They were weak-strawed and low-yielding; some of them at least had useful malting qualities, as, for instance, Scotch Common, with very low seed-dormancy and very rapid germination. About the middle of the century these were largely replaced by the similar but higher-yielding, woolly-rachilla variety, Chevallier, and this in turn at the end of the century by the denser, narrow-eared form Archer and by the broad-eared Goldthorpe. These, however, still had the disadvantages of weak straw, and of a tendency to a slightly brittle rachis, which made clean threshing difficult. Goldthorpe had also the further drawback of a long and fragile ‘neck’ between the uppermost leaf-sheath and the base of the ear, which resulted in loss of grain by ears falling off before harvest.

These disadvantages were to a large extent overcome by crosses using Archer as a parent. In one of these, Spratt-Archer, the other parent was Spratt, an old, very broad-eared variety long grown on fen soils in E. England on account of its very stiff straw. In the other, Plumage-Archer, the cross was made with Plumage, a variety of Scandinavian origin somewhat similar to Goldthorpe. These two varieties, although different in type, Plumage-Archer being a broad-eared, and Spratt-Archer a lax narrow-eared barley, were very similar in yield, in high malting quality and in their field characters, although Plumage-Archer was suited to rather heavier soils or higher rainfall than Spratt-Archer. Their high quality soon made them the most widely-grown varieties, and by 1940 they were together responsible for 80% of the malting barley area; they both remained on the Recommended List until 1960. Although very satisfactory from the traditional British maltster's point of view, they were still barleys which were difficult to grow satisfactorily; both were weak-strawed by modern standards, and both were late-maturing and profitable only if the sample reached malting standard.

Meanwhile important developments had taken place in continental Europe. Gold, derived from a Swedish land-race, was crossed with derivatives of the Czechoslovakian barley Hanna to give Kenia (introduced into Britain 1932, and recommended up to 1954), Maja and other similar cultivars. These may be said to have revolutionized British barley growing; they were higher yielding, shorter and stiffer strawed and earlier maturing than the older cultivars. They thus transformed barley from a rather hazardous specialist crop into a relatively easily grown general purpose crop which could profitably be grown for livestock feeding. They had been bred as malting barleys, but for continental malting and continental beers, and in Britain they were regarded as of very low malting quality. They, and later their derivatives such as Freja (recommended 1950–65) and Rika (1954–65), came to be grown extensively in Britain as feeding barleys.

As might be expected, the next step was to try to combine the high malting quality of the British barleys with the very desirable field qualities of the continental. Numerous crosses were made, of which Proctor (1952–77) was an outstanding success. Bred from Kenia × Plumage–Archer by Dr Bell at Cambridge, it outyielded the then available continental barleys, although it was rather later maturing, and was of even higher malting quality than its British parent. It came by 1960 to occupy the same commanding position in Britain that Spratt-Archer and Plumage-Archer had held earlier, and was widely used as a parent; six Proctor derivatives were in the 1976 Recom-

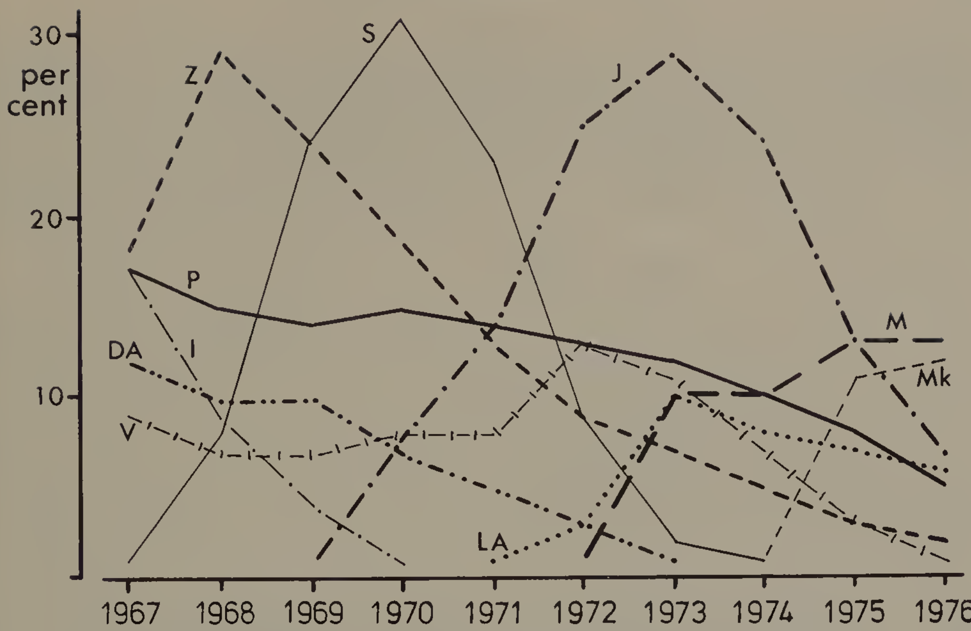


Fig. 30. Changes in popularity of spring barley cultivars over a ten year period. The figures are for numbers of samples of the particular cultivar submitted to the Official Seed Testing Station, expressed as a percentage of the total barley samples submitted during the year. In the period covered Proctor is in the later stages of its very slow decline, while Zephyr, Sultan and Julia successively reach their peak of popularity and fall again rapidly, to be followed by Mazurka and Maris Mink. DA, Deba Abed; I, Impala; J, Julia; LA, Lofa Abed; M, Mazurka; Mk, Maris Mink; P, Proctor; S, Sultan; V, Vada; Z, Zephyr. Data from N.I.A.B. *Annual Reports*.

mended List, including the substantially higher-yielding and equivalent quality Ark Royal (1976–).

Continental developments of Gold derivatives such as Vada (1969–76) and of crosses between Gold, Hanna, and a number of German two-rowed barleys, including Pflugs Intensiv from the Saar which provided a source of mildew resistance, gave rise to cultivars such as Zephyr (1966–76), Europa (1965–8) and Deba Abed (1965–74), parents of many of the varieties introduced in the 1970s, some of which are of as high malting quality as Proctor. As with wheats, genetic disease resistance has necessarily played an important part in the recent history of barley cultivars. For resistance to mildew, for example, breeders have used genes derived from the Saar barley mentioned above, from a smooth-awned form, from *Hordeum spontaneum*, from Indian and Arabian barleys and others, often combining genes from several sources to give resistance to as many fungal races as possible.

In some Scandinavian countries the cultivation of winter barley was prohibited as being responsible for the carry-over of disease from one spring crop to the next, but such a ban would be ineffective in

Britain, since the climate here allows volunteer plants of spring cultivars, which can never be wholly avoided, to survive the winter, and thus pass on disease. Winter barleys have not however in the past shown any markedly higher yield than spring barleys, and up to about 1971 occupied only some 10% of the British barley area. This figure rose to about 18% by 1977, probably as a result of increased interest in stubble-sown forage crops, and to some 31% in 1979; the German figure was about 80%. The first satisfactory winter two-rowed malting barley to be developed in Britain was Pioneer (1945–67), a cross between Spratt-Archer and a German two-rowed winter barley; this by crossing with Proctor gave Maris Otter (1965–), the most important winter barley in Britain in the early 1970s, which in turn gave rise to Maris Trojan (1975–); both these are malting barleys. Maris Otter had the disadvantage of marked susceptibility to *Rhynchosporium* leaf blotch, an increasingly serious disease in areas of high humidity, and particularly so on winter and early-sown spring crops. Although Proctor and a few other two-rowed cultivars showed fair resistance to this disease, good resistance was available only in six-rowed winter barleys, and from the early 1960s a number of these, mainly of German origin, came into use as feeding barleys. They were then the highest yielding of all available cultivars, but they, and particularly the earlier introduced ones such as Dea (1964–9), had excessively thick lemmas and were not popular with feed-millers. Two-rowed winter feeding barleys with the good *Rhynchosporium* resistance of the six-rowed later became available in cultivars such as Sonja (1975–) and Igri (1977–). This good resistance was not commonly found in spring barleys, and only the French cultivar Clermont, a six-rowed spring barley resulting from a cross between a Gold derivative and a six-rowed winter, showed it until the introduction of Armelle (1974–), a two-rowed malting quality derivative of Clermont.

The main diseases affecting the choice of barley cultivars are, in addition to *Rhynchosporium*, yellow and brown rusts, loose smut and mildew; this latter very important disease can be controlled by the use of systemic fungicides, but since some fungal races have tended to develop tolerance of the fungicide ethirimol, attention to genetic resistance is still necessary. Cereal cyst eelworm may be a problem in some areas; genetic resistance to this is available in the Danish cultivar Tyra (1976–).

The same possibilities of producing hybrid cultivars exist as with wheat, and some barleys of this type have been developed in the U.S.A., using however chromosomal rather than cytoplasmic male sterility.

OATS

Oats belong to the genus *Avena*, characterized by the inflorescence being a panicle, few-flowered spikelets, with large, thin glumes enclosing the florets. They are distinguished from the oat grasses and other members of the tribe *Aveneae* by their annual habit and large, pendulous spikelets.

The panicle is always of the spreading type, with comparatively long internodes and branches, but considerable variation occurs in its shape. The spikelets are usually three-flowered, and the glumes thin, multi-nerved and enclosing the florets. In the wild species and most cultivated forms, the caryopsis remains enclosed within the stiff, tapering lemma and the palea. The structure of the grain base and of the rachilla varies considerably in the different species and will be discussed separately. The awn if present is dorsal and often strongly geniculate.

The caryopsis resembles that of wheat in general structure, but is longer and pointed at both ends; the pericarp is hairy over the whole surface, and not merely at the tip as in wheat. On germination three seminal roots only are usually produced; the seedling also differs from that of wheat in that the region below the origin of the coleoptile elongates to form the so-called 'mesocotyl'. The complete absence of auricles distinguishes oats in the vegetative stage from the other cereals; the leaves are usually twisted in an anti-clockwise spiral, and have from eleven to thirteen nerves.

OAT SPECIES

A polyploid series exists in the genus *Avena*; the basic chromosome number is seven, and diploid species with fourteen, tetraploids with twenty-eight, and hexaploid species with forty-two chromosomes occur. Size of spikelet increases with increased chromosome number, but wild and cultivated forms are found in each group. The polyploid series presumably arose entirely in the wild, and not, as in wheat, partly as a result of cultivation. Evidence on the sources and inter-relations of the various species is however very scanty.

DIPLOID SPECIES

Avena strigosa Schreb. **Bristle-pointed Oat**

Spikelets small, lemma narrow and tapering into two awn-like points, dorsal awn also present, caryopsis small. Probably originally western Mediterranean in distribution; formerly cultivated apparently in

Fig. 31. Diploid oats. 1, whole spikelet. 2, spikelet without glumes. 3, lower grain (ventral view) of A, bristle-pointed oat (*Avena strigosa*); B, short oat (*A. brevis*). All ×3.

western Europe only. Its occasional occurrence as a weed in Britain is probably due to persistence from cultivation, which appears to have been widespread in earlier centuries, and included pilcorn, a naked form of this species now lost. The diaspore of the more usual hulled form is unsuitable for drilling and cultivation of this species is now obsolete; it persisted until the middle of this century on the extreme margin of arable cultivation in Wales and Shetland.

Avena brevis Roth., short oat, was a very similar form, but with shorter broader grains, formerly cultivated in south-western Europe. Both it and *A. strigosa* appear to be cultivated derivatives of the very similar *A. hirtula* Lag., a wild plant of Mediterranean coastal regions, with which they are interfertile. It differs in that the florets are each articulated at the base, so that the individual grains shed readily as soon as ripe.

TETRAPLOID SPECIES

These are of relatively little importance, and none occurs either wild or cultivated in Britain. *A. barbata* Brot., slender oat, resembling *A. hirtula*, but taller-growing and with shorter awn-points, is wild in the

Mediterranean area and naturalized in California, where it is utilized as a forage-grass, not as a cereal; *A. abyssinica* Hochst. is cultivated to some extent in Ethiopia. Both appear to be modified autotetraploid derivatives of *A. hirtula*. There are in addition two other Mediterranean wild tetraploids, *A. magna* Mur. et Terr. and *A. murphyi* Ladiz.. These both have large broad spikelets in which disarticulation takes place at the base of the lowest floret only, so that the diaspore consists of the whole spikelet minus the glumes.

WILD HEXAPLOID SPECIES

Three wild hexaploid oat species may be distinguished; these are *A. fatua*, the common wild oat, important as a widespread weed in Britain, *A. ludoviciana*, winter wild oat, of recent introduction from southern Europe, but now important as a weed in southern central England, and *A. sterilis*, the wild red oat, a Mediterranean weed. All three are interfertile, and no doubt had a common origin; they are probably allohexaploids, with two of the three genomes derived from large-grained tetraploids of the *A. magna* type, and the third perhaps from *A. hirtula* or some similar diploid.

Avena fatua L. **Common (Spring) Wild Oat**

Panicles large, closely resembling those of the common cultivated oat, spikelets usually of two grains, with special *articulation surfaces* at the base of each. These form joints which readily separate, so that the grains are shed as soon as the caryopsis is mature and the two

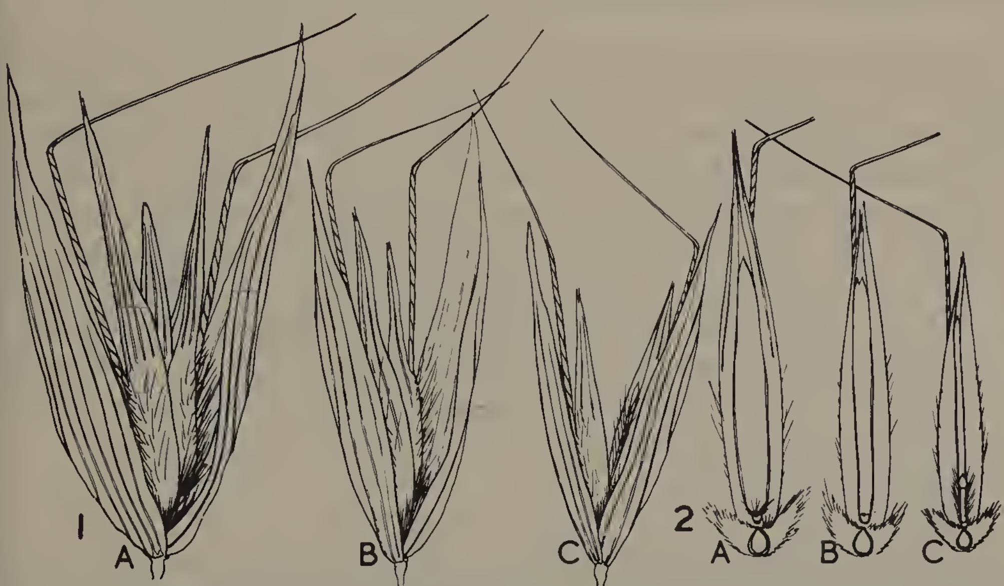


Fig. 32. Wild oat species. 1, whole spikelet. 2, lower grain in ventral view. A, *Avena sterilis*. B, *A. ludoviciana*. C, *A. fatua*. All ×2.

grains fall separately. Each grain has a tapering lemma with the lower half covered with stiff brown hairs, which are particularly conspicuous around the rachilla and the oval scar of the articulation. Each grain bears a strong dorsal awn; the tip of the lemma shows two minute blunt teeth. Grains germinate erratically and may show prolonged dormancy; the main peak of germination is in the spring. The common wild oat has been long established in Britain, but occurs only as a weed of crops, and was presumably originally introduced as an impurity of seed corn.

Avena ludoviciana Dur. **Winter Wild Oat**

This species closely resembles *A. fatua*, but can be distinguished by the two or three grains of the spikelet falling together; there is an articulation surface at the base of the lower grain only. If the grains separate, they do so by fracture of the rachilla above the base of the lower grain, and not by disarticulation. Germination is delayed and erratic as in *A. fatua*, but tends to take place mainly in winter rather than in spring. This wild oat species has only been comparatively recently recorded in Britain; it is a weed species of S. Europe and appears to have been introduced, probably with imported seed-corn, at some time prior to 1920. It is now widespread in southern central England. It is sometimes regarded as a hardy small-grained form of *A. sterilis.*

Avena sterilis L. **Mediterranean Wild Oat;** Wild Red Oat

This species is similar in structure to *A. ludoviciana*, but has a much larger spikelet and grains; it is a weed of the Mediterranean area, and does not occur in Britain. Its strongly-geniculate awns show very conspicuous movements with changes of moisture content, giving it the name of 'animated oat'. These movements of the awns result in the whole diaspore moving on the ground surface; if it enters a crevice its pointed base and barbed shape prevent withdrawal, and the whole structure is thus a very efficient self-burying diaspore. *A. sterilis* is very variable, and occurs in primary habitats such as sparse dry woodland as well as spreading as a weed of cultivation.

Wild oats as weeds

All three species of hexaploid wild oats are important as weeds, although only the first two are established in Britain. Their very close similarity to the cultivated cereals in structure, life-history and

requirements means that they are serious and difficult weeds, particularly in cereal crops, but also of importance in other arable crops. In wheat and barley they are inconspicuous in the vegetative stage, and in oats indistinguishable, and it is only after ear-emergence that their long straw and large panicle betrays their presence. Shedding takes place very soon after ripening, but usually not all grains are shed by harvest time, and consequently both soil and harvested grain are contaminated. Shed grains may remain dormant in the soil for a long period, a small proportion germinating each year for many years. Grains contaminating the crop are very difficult to remove completely from wheat or barley, and almost impossible from oats; passage through the combine normally breaks apart the adherent grains of *A. ludoviciana* (and of *A. sterilis* in countries where this occurs) and removes most of the large awns.

Spread of wild oats as seed impurities is checked by very stringent rules under the 1976 regulations for cereal, fodder plant and oil and fibre plant seeds, which require specified large samples to be free from wild oat 'seeds'. Control of growing wild oat plants may be attempted by hand roguing where the number of plants is small; by cultivations in bare ground or row crops; by the use of winter sown crops where spring wild oats are concerned and spring sown crops where winter wild oats; or by the careful use of suitable selective herbicides such as, in wheat or barley, tri-allate (soil application), difenzoquat or barban (foliar spray), or (as a foliar spray usable also in some varieties of cultivated oats) chlorfenprop-methyl.

CULTIVATED HEXAPLOID OATS AND THEIR ORIGIN

Two series of cultivated hexaploid oats exist, ***A. sativa*** L., the Common Oats of cool climates, and ***A. byzantina*** Koch, Red Oats, the main cultivated oats of warmer climates. In both, the articulation has been lost, so that the grain is not readily shed. In *A. sativa* fracture of the rachilla occurs (on threshing, or when over-ripe) at the top of the internode, i.e. just below each grain; in *A. byzantina* the fracture between the grains tends to be close above the lower grain, so that part of the rachilla forms a 'stalk' on the second grain. Remains of an articulation may sometimes be made out on the lower grain. *A. sativa* is usually regarded as representing the cultivated derivations of *A. fatua*, and *A. byzantina* those of *A. sterilis*; the species will, however, cross together, and fatuoid oats (i.e. forms resembling *A. fatua*) arise not infrequently by mutation from cultivated varieties, and all four species have probably had a common origin. There is no evidence for the cultivation of oats at a very early date, and it appears probable

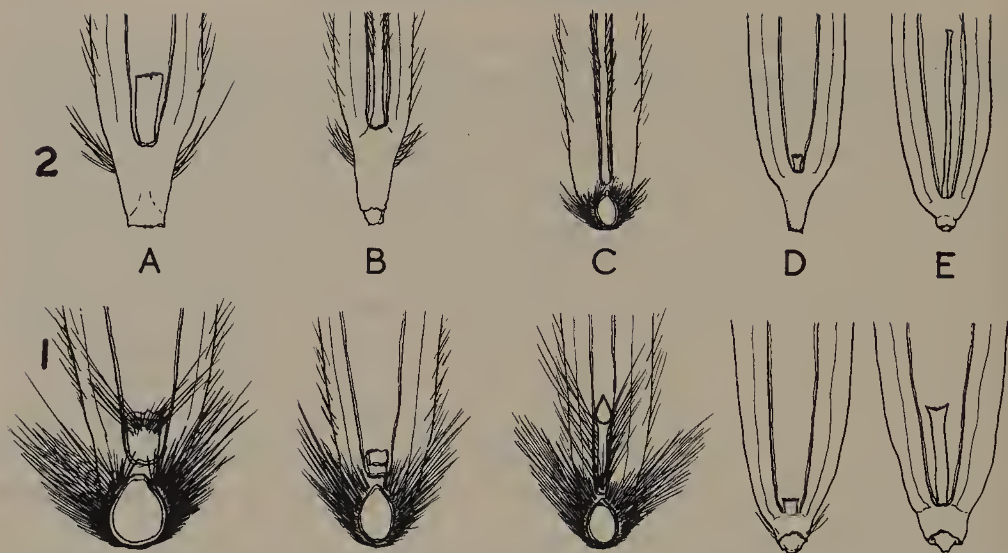


Fig. 33. Hexaploid oat species; grain bases to show method of separation. 1, base of lower grain in ventral view; 2, of second grain. A, *Avena sterilis*. B, *A. ludoviciana*. C, *A. fatua*. D. *A. byzantina*. E, *A. sativa*. All ×5.

that, like rye, oats originated as a secondary crop, first appearing as weeds of wheat and barley crops in S.W. Asia, perhaps 2 000 years ago, and being carried westwards and northwards. The process of harvesting and sowing seed would eliminate by gradual automatic selection the long-dormant forms and those shedding readily. Under the cooler and more humid conditions of N. Europe the *A. sativa* forms became the predominant cultivated oats, while further south the heat-resistant *A. byzantina* forms were more important. This latter group, the red oats, are still important in the warmer oat-growing areas, and show some disease-resistant characters not found in the common oat *A. sativa*. In Britain they are never grown as such, and are of interest only as parent material for the production of crosses with the common oat.

CHARACTERS OF AVENA SATIVA, COMMON OAT

Winter and spring forms. Winter oats have a very low vernalization threshold, and are thus not clearly distinguished in cold requirement from spring oats. They are however slower growing, and if sown after February will come to harvest late and give low yields. They are hardier than spring forms, but none shows extreme hardiness, and winter oats are confined to the southern half of Britain and to other areas with comparatively mild winters. The old variety Grey Winter, from which all modern winter cultivars have been derived, was very distinct in its vegetative habit as a young plant, being free-tillering

Fig. 34. *Avena sativa.* A, spreading panicle, equilateral (Golden Rain). B, dense, one-sided panicle (Black Tartar). $\times\frac{1}{2}$.

and almost prostrate, with the leaf-blades fringed with hairs. Spring oats are more upright in habit as young plants, and the leaves are usually glabrous.

Panicle characters. The panicle branches, although they arise on one side of the main axis at any one node, spread out around the axis; the branches at the lower nodes are longer than those at the upper nodes, so that the general form of the panicle is conical. The most noticeable departure from this form was in the old Tartarian oats such as Black Tartar where the branches were much more erect and tended to stand to one side of the axis; many of the cultivars derived from crosses between Tartarian and other oats had panicles intermediate in form between that of Black Tartar and the usual equilateral type. Equilateral panicles vary in size and shape and in number and size of spikelets, from, for example, the large open panicle of Grey Winter with numerous small spikelets to the small closed

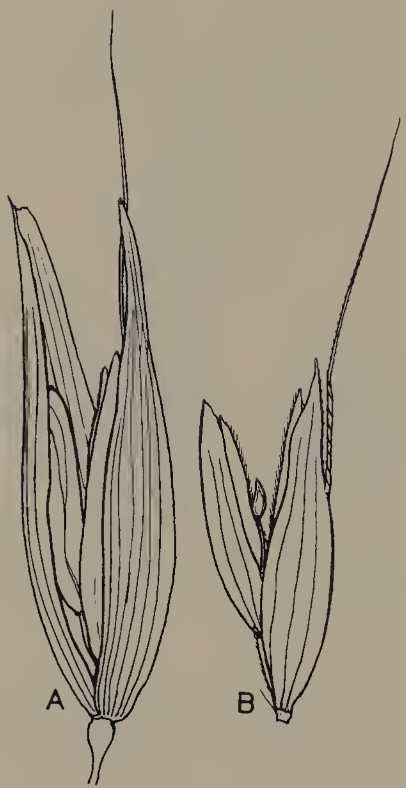


Fig. 35. Cultivated oats, *Avena sativa* (Grey Winter). A, whole spikelet. B, spikelet without glumes, showing awned lower grain and abortive third floret. ×3.

one of most of the modern spring oats, with fewer larger spikelets.

Variation also occurs in the number of grains per spikelet. Usually there are three florets present, of which the lower two each produce a caryopsis; this gives a large basal grain, a rather smaller second grain, and an abortive upper floret which remains minute. Greater evenness in size of grain is obtained where, as in the old variety Potato, only the lowest floret produces a caryopsis; this however results in a lower yield, and one-grained forms are obsolete. In some forms three grains are produced, but this results in even greater disparity in grain size, without markedly increasing yield. Only in the naked oats does the number of florets normally exceed three or four; these are rather distinct forms with thin lemmas similar in texture to the glumes, which allow the caryopsis to thresh out very readily. Seven or eight florets are borne on a long lax rachilla, so that the upper ones stand out well beyond the glumes. Naked oats have been used in China for human food, but are not grown in Britain. They would have distinct advantages for oatmeal production and for poultry feeding, but the problem of pre-harvest shedding of the very loose caryopsis has so far

Fig. 36. Naked oats. A, single spikelet. B, single floret, ventral view. C, threshed caryopsis. All ×2.

proved insoluble. A number of cultivars have been produced, but none which can be safely left until mature enough to harvest by combine.

In all cultivars other than the naked oats the threshed grain consists of the caryopsis, more pointed than that of wheat and with the whole pericarp surface hairy, enclosed by the palea and the rather stiff lemma. One internode of the rachilla is present; in second grains of the spikelets this usually retains the abortive third floret at its tip. A sample may contain a few double grains, in which the lemma margins of the lower grain are wrapped around the second grain, so that it does not separate. The lemma is glabrous or almost so in all the cultivated oats, with at most a few hairs on the base or on the rachilla. The colour, in older cultivars, could be black (e.g. Supreme), grey (e.g. Grey Winter), yellow (e.g. Golden Rain) or white as in all modern cultivars. Awns are rare in most modern cultivars; some have a rather weak dorsal awn on the lowest lemma only, and that only in some spikelets.

Cultivar distinction

Modern oat cultivars tend to be very similar in their major characters, and their identification involves the use of minor differences such as:

Panicle. Shape, size, arrangement of branches (difficult to determine except in the standing crop; panicles cut and stored are often distorted). Hairiness of culm node.
Spikelet. Attitude, size of glumes and colour before ripeness. Frequency of three-grain spikelets.
Grain. Size and shape; shape of basal fracture and number of basal hairs. Length, shape and hairiness of rachilla. Frequency of awns.
Field characters. Growth habit as young plant; presence of hairs on leaf-sheath and on margin of leaf-blade. Leaf attitude at ear emergence.

Grain quality and uses

The oat caryopsis is of high feeding value with some 14% protein, 7% oil and 65% carbohydrate, with a digestible organic dry matter (DODM) percentage of perhaps 72. The feeding value of the lemma and palea (husk) is of course much lower, with negligible protein, some 35% crude fibre, and DODM of 33% or less. The value of the whole grain for feeding therefore depends very much on the ratio of husk to kernel (caryopsis); the husk percentage varies from rather over 20% in the highest-quality oats to about 35% in the lowest. It is largely genetically controlled, that is it is a cultivar character, and the N.I.A.B. lists score oat cultivars for kernel content, but it is to some extent affected by climatic conditions, and husk percentage may be lower in Scottish-grown oats than in the same cultivar grown in southern England.

For human consumption as oatmeal the lemma and palea are removed by splitting off between widely set millstones. Some fragments of lemma may be left, and for this reason only white oats are acceptable for oatmeal production. The caryopsis contains oil in the endosperm as well as in the embryo, and lipases are present in the pericarp. These fat-splitting enzymes must be removed, since they could lead not only to rancidity of the oat oil, but if incorporated in oat products could hydrolyse other fats added as shortening agents, with the production of off-flavours and of soaps formed from the interaction of free fatty acids and baking soda. The lipases are either removed by complete removal of the pericarp by a process of wet brushing, or inactivated by steaming. If the latter method is used, a

light brushing is necessary to remove the pericarp hairs. The treated caryopsis (groat) is cut to give pinhead oatmeal, which can be further stone ground for fine oatmeal, or rolled and cooked for rolled oats. Although the protein content is higher than in wheat, the proteins do not form gluten and oat flour is not used for bread.

OAT CULTIVARS IN BRITAIN

The cultivation of oats in Britain is of much later date than that of wheat or barley, and although some grains have been found dating from Roman times these may well have been chance impurities. Oats were probably introduced as a crop during the Middle Ages, but there is little firm evidence available. The diploid bristle-pointed oat, perhaps mainly in its naked form pilcorn, was used for human consumption as well as the common oat; the use of oats for human food was developed mainly in the north and west in areas less suited to wheat. At a later period oats were used largely for livestock feeding, often fed whole in sheaf without threshing. Oat straw was highly valued and regarded as considerably better for feeding than wheat or barley straw. This was largely due to the fact that oats were cut at an early stage of ripening, while the straw was still partly green, in order that the grains, which on a large panicle show a somewhat greater range of ripening date than those on a compact spike, should have time to mature evenly while standing in stook. With modern oats, harvested by combine, the straw does not show any superiority. By the nineteenth century some varieties such as Potato (introduced 1788) and Sandy (1824) were in fact spoken of as ‘straw producers’, since they gave a greater yield of straw than of grain, and contrasted with the newer ‘grain producers’. This distinction was apparently valid at very low levels of fertility, but later trials showed that with even moderate manuring these latter varieties outyielded the ‘straw producers’ in straw as well as in grain.

By the latter part of the nineteenth century Grey Winter was the main winter oat; among spring oats the varieties included Black Tartar, apparently of eastern European origin, various derivatives of crosses of this with Potato and Grey Winter, and a number of local land-races. All these were long-strawed and low yielding, and they were replaced by continental forms, mainly selections from the Probsteier land-race of northern Germany and southern Denmark, and crosses between these selections. Among the first were Victory (introduced 1908) and Golden Rain (1903, both recommended up to 1953) followed by Star (recommended 1933–54) and Eagle (1935–57), both Victory derivatives, and these in turn by Sun II

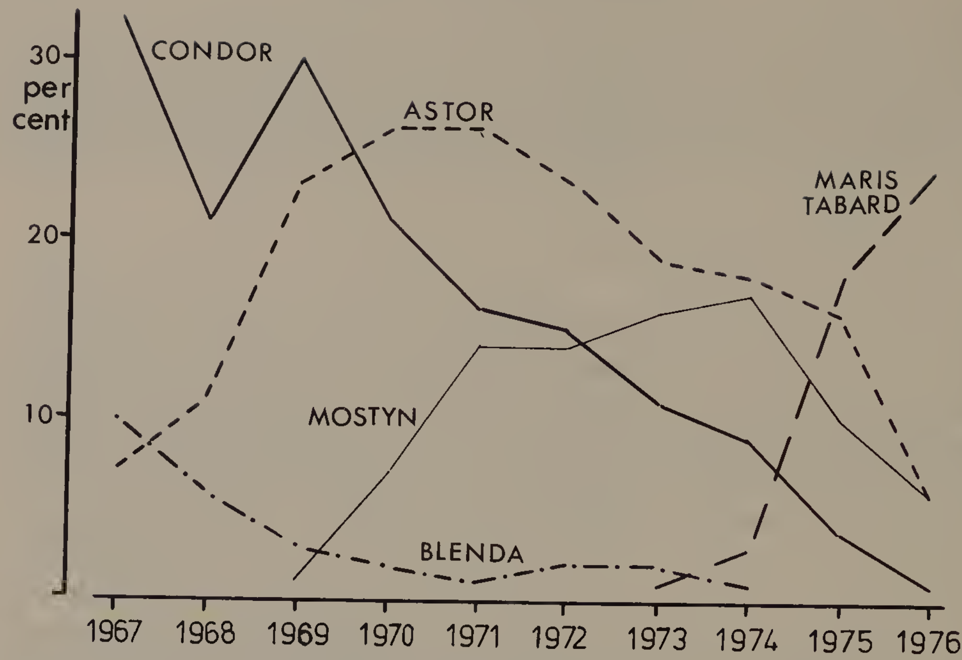


Fig. 37. Changes in popularity of selected spring oat cultivars over a ten year period. The figures are for numbers of samples of the particular cultivar submitted to the Official Seed Testing Station, expressed as a percentage of the total oat samples submitted during the year. The curves show Condor falling from its peak popularity, the last stages of the decline of Blenda, the rise and fall of Astor and Mostyn, and their replacement by Maris Tabard. Data from N.I.A.B. *Annual Reports.*

(1950–62) and Blenda (1952–65), both derived from Star × Eagle crosses. These again were superseded by the related and similar but higher-yielding Astor (1962–75) and Condor (1960–75), and the spring oats recommended in 1977 were for the most part derivatives of one or other of these. In these later varieties genes from *A. byzantina, A. ludoviciana* and other sources of disease resistance have been incorporated.

The spring oat picture has thus changed during the twentieth century, in that cultivars of continental origin have come to replace those formerly used in Britain. This change was much slower in the north, and varieties derived from Potato and Black Tartar such as Supreme (from 1915), Onward (from 1935, both recommended in England up to 1954 only) and Forward (introduced 1953, not recommended in England) remained popular in Scotland and in hill areas. Supreme and a few other varieties with black lemmas, abandoned in favour of white oats over most of the country, perhaps owed their continued popularity in the hills to the fact that they showed the effects of poor harvest conditions less conspicuously than white oats.

Winter oats can all be regarded as improved derivatives of the very old variety Grey Winter. This was the sole source of winter hardiness,

but had very long weak straw and was not suited to any but soils of quite low fertility. Initially shortness of straw was derived from a Cyprus oat to give first S 81 (introduced 1931), the first of a series of oat cultivars bred at Aberystwyth, and at a later period S 172

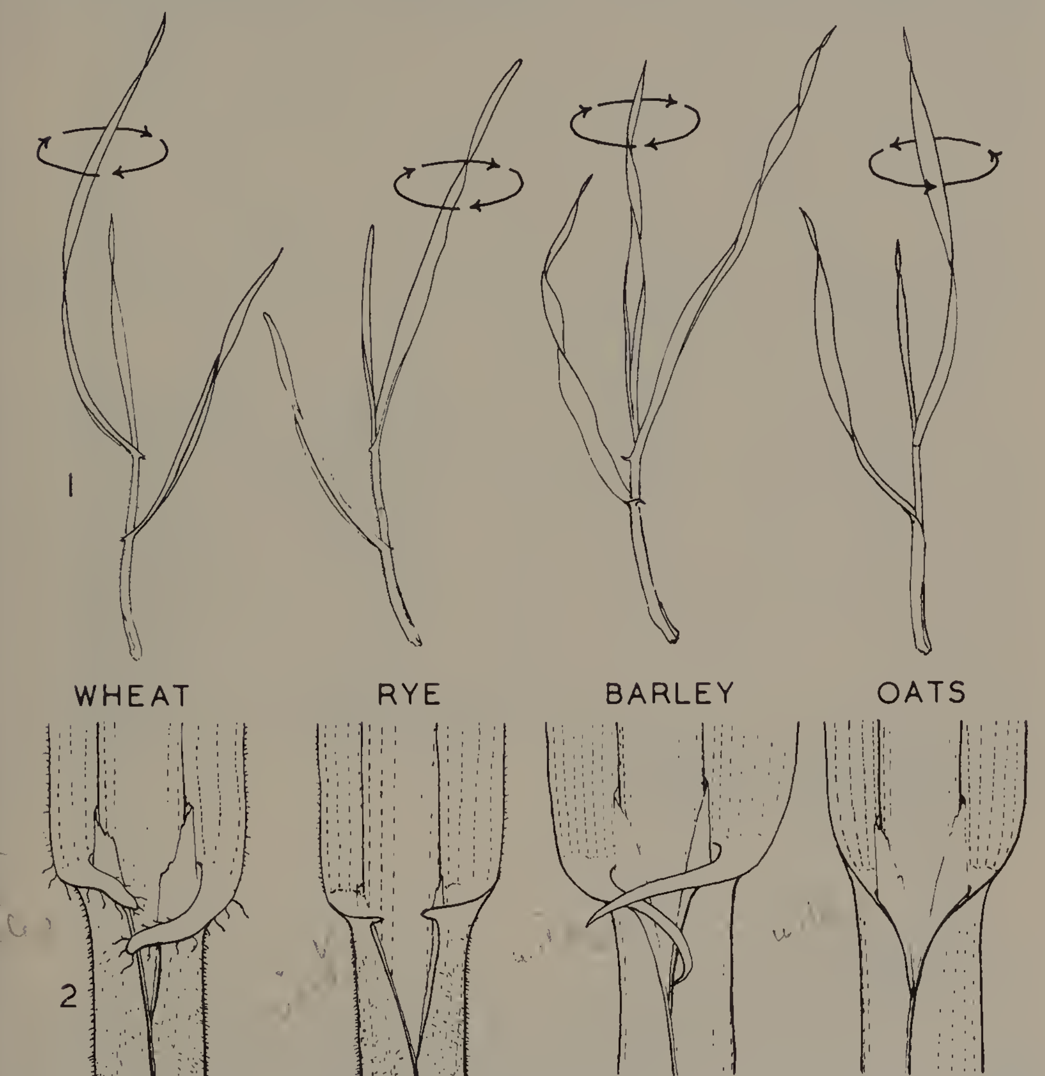


Fig. 38. Characters for recognition of common cereals in vegetative stage. 1, single tiller of young plant, $\times\frac{3}{8}$. 2, junction of leaf-sheath and blade, $\times 6$.

WHEAT: auricles blunt, hairy; leaf-sheath and blade always hairy. Ligule medium length. Blades with about 12 veins, twisted clockwise.

RYE: auricles very short, not hairy; leaf-sheath and blade variably hairy, greyish. Ligule short. Blades with about 12 veins, twisted clockwise.

BARLEY: auricles long, slender, glabrous; leaf-sheath and blade usually glabrous (scattered long hairs in a few varieties). Ligule medium length. Blades with about 20 veins, twisted clockwise.

OATS: auricles absent; leaf-sheath and blade usually glabrous, scattered long hairs in some varieties, especially of winter oats. Ligule medium length. Blades with about 12 veins, usually twisted anti-clockwise.

(recommended 1945–65). This latter variety had extremely short straw, but was rather low-yielding and of low quality. A cross of Grey Winter with Marvellous, partly a Potato derivative, had given the better quality but still rather long strawed S 147 (1938–62); this crossed with S 172 gave Powys (1958–66), of good quality and more satisfactory straw length. From this cross, or one or other of the parents, most of the winter oats of the 1977 Recommended List were derived, with disease resistance added as in the spring oats.

The same problems of race-specific resistance to mildew arise as with wheat and barley; the other important oat disease is crown rust, but this is largely confined to Wales and south-western England. Eelworm damage can be serious; resistance to stem eelworm is found in Grey Winter and many of its derivatives, resistance to cyst eelworm in the Swedish cultivar Nelson (1973–).

As with wheat and barley, oat yields doubled during the period from say 1910 to 1976, and the average oat yield is very similar to that of barley, although of course the greater husk percentage of oats must be taken into account. Nevertheless, the oat area in England and Wales fell during this period from about 850 000 to about 235 000 hectares. This is essentially due to the fact that up to the beginning of the twentieth century oats were largely grown for feeding to horses; the replacement of horses for transport, and then in the 1940s their virtual disappearance from agriculture, resulted in the massive changeover to barley, found more satisfactory as a feeding cereal for dairy cows and beef animals.

RICE

Oryza sativa L. **Rice**

Rice is not closely related to any of the other cereals, and is a member of the tribe *Oryzeae*, of which the only British representative is a rare plant of wet places, cut-grass, *Leersia oryzoides* (L.) Swartz. The inflorescence of rice is a panicle with numerous functionally one-flowered spikelets. The glumes are almost absent, being reduced to small facets at the base of the spikelet, but a pair of small extra empty lemmas, representing the remains of two lower florets (cf. *Phalaris*, p. 182) are found at the base of the lemma and palea of the fertile floret. These are both large, stiff and almost woody, keeled and rough on the outer surface. The lemma bears a terminal awn in many varieties. The flower is unusual in having six stamens. Lodicules are present and the floret opens for about half an hour at anthesis; self-pollination is usual, but up to about 0·5% crossing may occur.

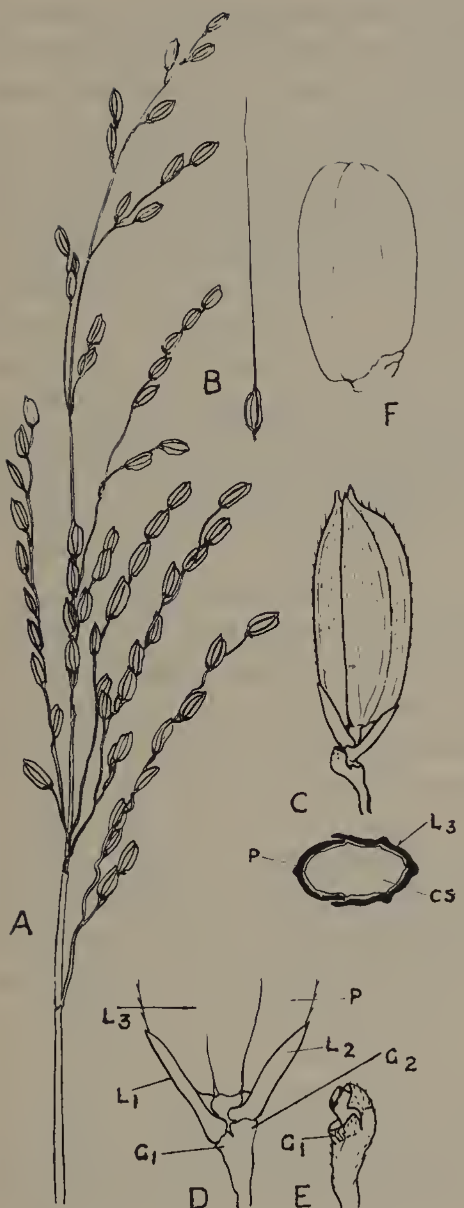


Fig. 39. Rice. A, panicle of awnless variety, $\times\frac{1}{2}$. B, single spikelet of awned variety, $\times\frac{1}{2}$. C, single spikelet $\times 3$, in side view and diagrammatic cross-section. D, base of spikelet, $\times 7$. E, base of rachilla, and vestigial glumes, $\times 10$. F, caryopsis after hulling (soaked), $\times 4$. G_1, G_2, glumes. L_1, L_2, sterile lemmas. L_3, fertile lemma. O, palea. CS, caryopsis.

Vegetatively rice resembles the temperate cereals in having narrow leaf-blades; the sheaths are split, and a short ligule and very narrow toothed auricles are present. It is usually grown on land which is kept flooded for the greater part of the growing period, and both roots and leaves show the very large intercellular air-spaces characteristic of water plants.

Rice is a plant needing high temperatures (germination minimum about 13°C, optimum 30–35°C), and its cultivation is therefore confined to the area between 40°N and 40°S latitude. Within this area it is

a major crop, particularly in south-eastern Asia; the total world area of the rice crop is second only to that of wheat, and far in excess of that of any of the other cereals. Varieties differ considerably in their water requirement; 'dry rice' includes those which can be grown on moist but not flooded soils, and usually gives lower yields than those grown in water. The usual method of cultivation involves sowing in special seed-beds and later planting out the young tillering plants in flooded fields; where, as in the southern U.S.A., the cultivation is mechanized, the seed is drilled and the ground later flooded, and finally drained again for harvesting. Yields vary up to about six tonnes per hectare of grain as threshed (i.e. including lemma and palea), but the average world yield is probably only about one-third of this. Yields are rising with the introduction of improved varieties and methods, and in the more favourable areas it is possible to obtain two crops per year.

The caryopsis does not thresh out, and the threshed grain (paddy) must be hulled to remove the lemma and the palea, which constitute some 20–25% or more of the total weight. The whole caryopsis (brown rice) can then be used for human consumption, but it is frequently polished to remove the bran and germ. The use of this polished rice, consisting of the whole endosperm only, is of course quite acceptable in western countries where it forms only a small part of a mixed diet, but can be disastrous in areas where rice is the staple food. Polishing removes some of the already low protein and oil content, but more importantly, removes also almost all the vitamin B1 (thiamin) content. The use of polished rice as a staple food thus leads to the very serious deficiency disease beri-beri. White wheat flour can be readily fortified with added vitamin, but polished rice, used whole and not as flour, presents a much more difficult problem, which has been only partially solved by parboiling before polishing, which allows some of the thiamin to diffuse from the bran into the endosperm, or by adding a small proportion of heavily fortified grains.

Rice cultivars show great variation in size and shape of grain and in texture of endosperm. 'Hard' rice, which is the most important type, with translucent vitreous endosperm, differs from 'soft' or glutinous rice, with opaque chalky endosperm, not in protein content but in starch composition. Hard rice has a high amylose content, glutinous rice high amylopectin. Varieties can be grouped into the northern *japonica* (subsp. *sativa*) and the southern *indica* (subsp. *indica* Kato) types, separated by partial sterility barriers. Wild forms such as *O. rufipogon* Griff. (*O. fatua* Koenig) are found in India, but there is not sufficient evidence to enable the origin of rice cultivation to be

determined. A distinct form still cultivated in West Africa, *O. glaberrima* Steud., may have originated there, independently from the Asiatic rices.

Zizania aquatica L., wild rice (in N. America), is an aquatic annual, the grain of which is collected for food; not usually cultivated. Panicle with male spikelets on lower branches, female on upper; spikelets one-flowered; 6 stamens in male.

MILLET

Millet is a name used for a number of different small-grained cereals belonging to various genera, mainly crops for local consumption, grown under conditions unfavourable to the major cereals.

Eleusine coracana Gaertn., **finger millet,** belongs to the tribe *Chlorideae,* with branched spikes of several-flowered spikelets, and is not closely related to the other millets. The fruit is not strictly a caryopsis, since the pericarp is loose and not fused to the testa; it is very small (*c.* 2 mm) and free threshing. Finger millet is widely grown on poor soils in central Africa and southern India; it is perhaps derived from the smaller weedy *E. indica* Gaertn.

The other cereals known as millets belong to various genera of the mainly tropical tribe *Paniceae,* with broad leaves with radiating mesophyll cells, spikelets dorsally compressed and composed of two florets, one of which is sterile. Three of the more important of these millets are described below.

Panicum miliaceum L. **Common Millet** or Proso Millet

This is an annual, growing some 60–120 cm high, with often unilateral panicles varying in compactness. The leaf-sheaths are split, ligules short, auricles absent, leaf-blades hairy, from 1 to 3 cm broad. Branches are frequently produced from nodes well above ground-level.

The panicle bears numerous spikelets, each with a pair of thin, membranous glumes, the inner larger than the outer. Within these are a lower sterile floret, with lemma similar in size and texture to the inner glume, and palea minute, and an upper fertile flower. This has, when mature, a short, rounded caryopsis some 3 mm long, with no ventral furrow and enclosed in the thick, shiny lemma and palea. The colour of the lemma and palea varies according to variety; white, yellow, grey and black forms occur.

Fig. 40. Millet, *Panicum miliaceum*. A, part of plant with unripe grain (spikelets shown only on some panicle branches) $\times\frac{3}{16}$. B, part of panicle, ×3. C, single spikelet and separate parts, ×7. G_1, G_2, glumes. SL, SP, lemma and palea of sterile floret. FL, FP, lemma and palea of fertile floret (the caryopsis remains enclosed between these).

Common millet is of uncertain origin; it has been suggested that it may have been derived from the Ethiopian *P. callosum* Hochst. but there are no records of its ancient cultivation in Egypt or south-western Asia, although it was widespread in southern and central Europe during the neolithic period, extending to northern Europe

(but not Britain) in the Bronze Age, and its cultivation is probably ancient in China. It is still used in eastern Asia for human consumption, but elsewhere tends to be replaced by higher-yielding, larger-grained cereals. It will ripen in southern England, but is not an economic crop; in North Africa it is used to some extent as a forage plant.

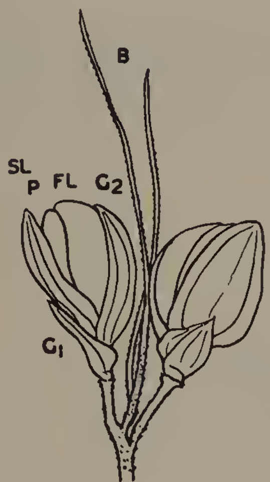


Fig. 41. Italian millet, *Setaria italica*; part of panicle showing bristle and two spikelets, ×7. B, bristles; G_1, G_2, glumes. SL, lemma of sterile floret. FL, P, lemma and palea of fertile floret.

Setaria italica (L.) Beauv. (*Chaetochloa italica* (L.) Scribn.). **Foxtail Millet,** Italian Millet

This millet differs from *Panicum miliaceum* in having a more compact panicle, often cylindrical and spikelike. The structure of the spikelet is similar, but in addition a number of bristles, usually from one to three, are present below each; these represent reduced sterile spikelets (cf. *Cynosurus*, p. 156). The grain is rather smaller than that of common millet, and flattened on one side. Foxtail millet perhaps originated in eastern Asia; it is recorded as cultivated in China in the third millenium B.C., but there are Bronze- and Iron-Age finds from Europe. It is now widely grown as a dry area crop in subtropical regions, and especially in India and China. A form with a narrow cylindrical panicle is used as a forage grass in the U.S.A. under the name of Hungarian Grass; it resembles the wild species *Setaria viridis* (L.) Beauv., green millet, of southern Europe, which is an occasional casual in England.

Pennisetum americanum (L.) K. Schum. (*P. typhoides* (Burm. f.) Stapf and Hub.). **Bulrush Millet,** Pearl Millet

This is a tall annual up to 3 m or more, with very dense contracted

panicles, with the closely packed fertile spikelets subtended, as in *Setaria,* by stiff bristles. Cross-pollinated; caryopsis small, pale grey, free threshing. Probably tropical African in origin, widely cultivated in Africa and India; more tolerant of dry poor soils than sorghum, but less so than the other millets.

SORGHUM

The sorghums, forms of ***Sorghum bicolor*** (L.) Moench (*S. vulgare* Pers.), are warm-climate cereals which somewhat resemble millets, but are usually stouter plants with broader leaves. The structure of

Fig. 42. Sorghum. A, panicle, $\times\frac{1}{2}$. B, group of spikelets seen from outer and inner sides, $\times 3$: FS, fertile spikelet; SS, sterile spikelet. C, single fertile spikelet of awned variety in pre-flowering stage, dorsal and ventral views, $\times 7$. D, single fertile spikelet of awnless variety, with apex of mature caryopsis exposed, $\times 7$. E, threshed caryopsis, $\times 7$. F, as C, but dissected to show separate parts. G, G, glumes. SL, lemma of sterile floret. FL, FP, lemma and palea of fertile floret. F, flower.

the inflorescence is more complex, and the sorghums are placed in a distinct tribe, the *Andropogoneae,* to which sugar-cane also belongs. The spikelets are paired, with one pedicellate and male, the other sessile and hermaphrodite. The structure of the hermaphrodite spikelet somewhat resembles that of millet and the other members of the *Paniceae,* but the outer glume is as large as the inner, and both are hardened. The lower sterile floret is represented by the lemma only; the upper fertile floret has a narrow, bicleft, shortly-awned lemma, two lodicules, three stamens, and ovary with two long styles; the palea is absent or very small. Up to about 50% cross-pollination may take place; the threshed grain, which consists either of the whole fertile spikelet with the caryopsis enclosed, or of the naked caryopsis, is usually broadly oval and larger than the millets.

The sorghums, which are of African origin, are extremely variable in form and use; the main groups are:

(1) The grain sorghums, extensively grown in Africa for human consumption in a wide range of forms, durra, kafir corn, feterita etc., varying in grain shape and density of panicle. Introduced into the U.S.A. and there developed from tall cross-pollinated forms into short-strawed hybrid cultivars, high-yielding and extensively grown, mainly for animal feeding. Sorghums resemble maize in their high photosynthetic efficiency (C4 metabolic pathway) and in their range of endosperm textures; as in maize, a number of different types have been developed, including a waxy (amylopectin) form.

(2) The broom corns, a group of minor importance, with stiff open panicles used, after deseeding, for the manufacture of sweeping brooms.

(3) The sweet sorghums, or sorghos, grown for the high sugar content of the immature stem from which syrup can be extracted; grown largely for forage.

Sudan grass, *S. sudanense* Stapf (*S. arundinaceum* (Desv.) Stapf var. *sudanense* (Stapf) Hitchc.), is a related species grown as an annual forage grass; hybrids between this and *S. bicolor* have been developed for forage use.

Saccharum officinarum L., **sugar cane,** may be mentioned here, since it is related to sorghum, although not of course grown as a cereal. It is a perennial grass up to 5 m high, widely grown in the tropics for sugar, which is extracted from the stout solid stems. The inflorescence resembles that of sorghum, but the spikelets are all hermaphrodite; the caryopsis is very small (1–2 mm); sugar cane is

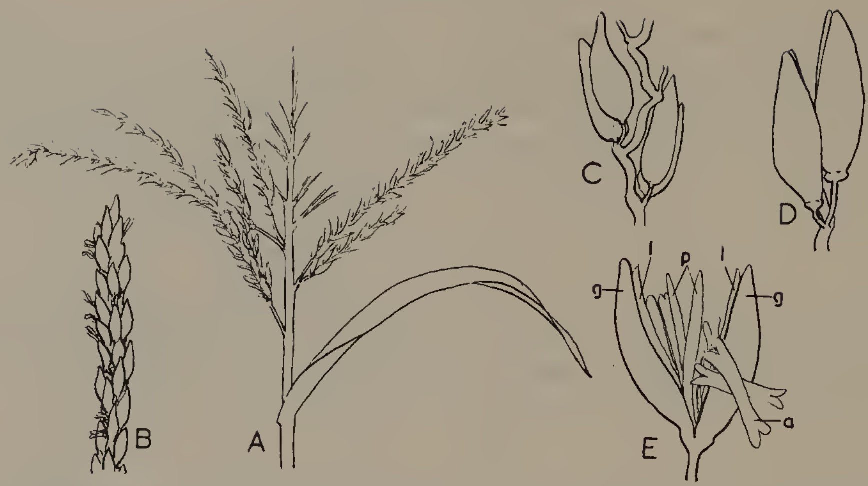


Fig. 43. Maize; male inflorescence. A, tassel (a few branches only shown in full), $\times\frac{1}{6}$. B, part of single branch of tassel, $\times\frac{1}{2}$. C, part of branch, $\times 1\frac{1}{4}$, to show arrangement of spikelet-pairs on rachis. D, spikelet-pair, $\times 1\frac{3}{4}$. E, single spikelet in flower, $\times 2$: *g*, glumes; *l*, lemmas; *p*, paleae; *a*, anther.

normally vegetatively propagated. The photosynthetic efficiency is high; yields of 200 tonnes of cane per hectare can be obtained from a two year old stand; with an extractable sugar content of 11–13% this is equivalent to some 13 tonnes of sugar per annum, i.e. about twice the yield from sugar beet under temperate conditions. Cultivated in southern Asia since the first millenium B.C.; perhaps originally derived from *S. robustum* Brandes et Jasw., wild in New Guinea. Yields have been much improved by breeding during this century; many modern cultivars show improved disease resistance derived from crosses with *S. spontaneum* L., wild in East Africa and southern Asia.

MAIZE

Zea mays L., **Maize**

Maize belongs to a small, highly-specialized tribe, the *Maydeae*, closely related to the *Andropogoneae*, but having male and female flowers in separate spikelets. It is an annual, usually producing only a single shoot, with stout, solid stem and very large leaves with broad blades. The terminal panicle bears only male flowers, and is known as the tassel. The panicle branches are long and bear closely-spaced, short-stalked pairs of spikelets. Each spikelet consists of a pair of glumes enclosing two male florets, each with lemma and palea, lodicules and three stamens. The male florets open widely and pollen is shed to be carried by wind to the female flowers. These are borne on special female inflorescences, the ears, in the axils of some of the

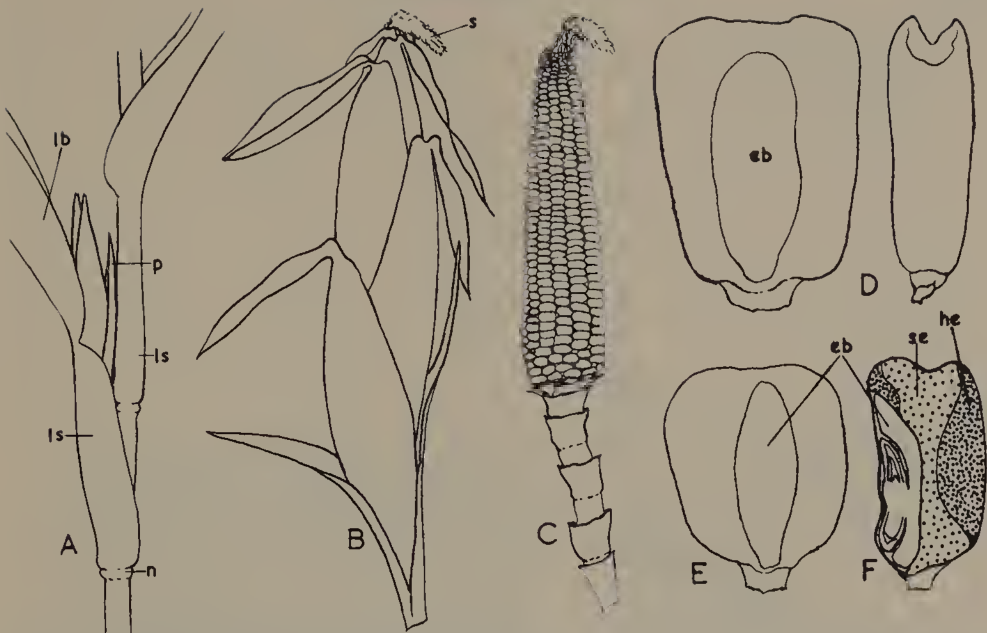


Fig. 44. Maize, female inflorescence. A, part of plant to show young ear in axil of leaf. B, almost mature ear (Goudster) surrounded by husk leaves. C, the same with husk leaves removed. All $\times\frac{1}{6}$: *n*, node at which cob is borne; *p*, prophyll of cob shoot; *ls*, leaf-sheath; *lb*, leaf-blade; *s*, withered silks (styles). D, grain of White Horse Tooth in face and side view; E, of Goudster. F, diagrammatic vertical section of dent-corn grain: *eb*, embryo; *he*, horny endosperm; *se*, starchy endosperm.

middle leaves of the main stem. Each ear consists of a short stout axis, the cob,* bearing at its lower nodes a series of closely-packed, imbricating, almost bladeless leaves forming the husk, and completely enclosing the upper fertile part. This is a dense spike with a number of vertical double rows of very much reduced spikelets; it may be regarded as representing the coalescence of a branched structure like the male inflorescence, each double row corresponding to the series of pairs of spikelets borne on one branch. Reduction of the spikelet has progressed so far that, in the mature inflorescence, all that is visible is a series of tightly-packed, naked caryopses. Only in the immature stage can it be made out that each grain has around it a series of scales, the two glumes and the two lemmas and two paleas of the two-flowered spikelets. These structures do not normally develop further, and their protective function is taken over by the husk leaves, which form a continuous and persistent cover to the whole ear. Pollination is made possible by the very great development of the single style of each ovary, which forms a long thread extending up from each flower to the apex of the husk, where the numerous threads emerge as a conspicuous tuft, known as the silks. The upper part of

* 'Cob' is also used, particularly in Britain, to mean the whole female inflorescence or ear.

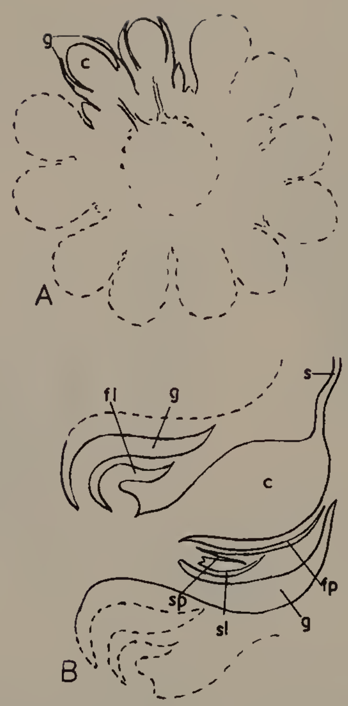


Fig. 45. Diagrams to show structure of maize ear. A, transverse section of young ear; one pair of spikelets only shown in solid line. B, vertical section through single spikelet before pollination: *g*, glumes; *fl*, *fp*, lemma and palea of fertile floret; *sl*, *sp*, of sterile floret; *c*, ovary; *s*, style.

each style is receptive, and wind-borne pollen germinates on its surface, the pollen-tube growing down through the whole length of the thread to reach the ovule. Growth of the style continues until pollination is effected, so that the styles may reach a length of 30 cm or more. After pollination the silks wither, and enlargement of the grain takes place. The husk leaves become dry and papery, but remain in position around the mature ear.

There is thus no normal means of seed-dispersal, and maize is not known as a wild plant. It was already an old-established cultivated plant in America in Columbus' time, but archaeological finds in Mexico and other evidence suggest that it was derived from a small multi-tillered plant, with terminal inflorescences with female spikelets at the base and male above. This primitive maize, dating to perhaps 5 000 B.C. and now long extinct, was a 'pod corn', that is the glumes and lemmas of the female spikelets were well developed—a character found in a few present-day forms of little economic importance. Crosses with *Euchlaena,* a still existing wild member of the same tribe, may have played a part in the development of cultivated maize.

Maize is, in warm climates, a very high yielding and adaptable cereal, and after the discovery of America by Europeans its cultivation spread rapidly to all suitable parts of the world. The minimum temperature for germination is 10°C, and seedling growth below

Fig. 46. Maize leaf, $\times\frac{1}{8}$.

13°C is very slow, so that it is not adapted to the cooler parts of the temperate zone. It has, like most of the grasses of related panicoid tribes, the C4 metabolic pathway and is photosynthetically highly efficient in conditions of high temperature and high light intensity. It shows a wide range of variation, from early dwarf forms some 1·5 m

high with about twelve leaves on the main shoot and maturing under favourable conditions in about ninety days, to forms 4 m high with perhaps twenty-five leaves and a growing season of some one hundred and ninety days. Ear size varies with from 8 to 28 rows of grains on the cob (commonly 12–18), with some 20–70 grains in each row up the length of the cob. If conditions are unfavourable the grains towards the apex of the cob remain undeveloped. The regular arrangement of grains in an even number of rows, derived from the vertical rows of paired spikelets, is usually conspicuous; only where, as in the old sweet corn variety 'Country Gentleman', both florets of the spikelets are fertile do the grains become crowded and the arrangement irregular.

The caryopsis is usually large, from about 8 to 18 mm long; the embryo, which contains about 50% oil, with a linoleic acid content of about 40%, is large in proportion, forming some 10–12% of the total caryopsis weight. The endosperm is starchy in the majority of forms, with some 10% protein in the whole grain. This protein is not gluten in the strict sense, and maize is not suitable for bread making. It has however come to be widely grown in the sub-tropics for human consumption, replacing sorghum in areas where sufficient water is available. In countries where wheat can be grown satisfactorily, maize is used mainly for animal feeding. Nutritionally maize is similar to the other cereals in many ways, but with one important exception; this is that its nicotinic acid (one of the vitamin B group) is not readily available and that the deficiency disease pellagra may therefore occur where maize forms the staple human diet.

Large scale milling of maize grain for human consumption can be either dry or wet. In the former method special conical rollers remove the germ (embryo) and bran (pericarp and testa), giving coarse grits (endosperm fragments), which can be roller milled to give fine grits and flour. From the separated germ oil is extracted, and used as an edible oil and for technical purposes. In wet milling the soaked grain undergoes lactic fermentation and treatment with sulphur dioxide, followed by degerming and fine wet grinding; the resultant slurry, after sieving out the bran, is separated into starch and protein fractions. These are dried to give corn * starch (known as cornflour in Britain) and maize 'gluten', which is used in animal feeding.

The structure and composition of the endosperm varies in different forms of maize. The main types are (1) flint maize, in which the whole of the outer part of the endosperm is hard and horny in consistency and the grain remains round-topped when ripe, and (2) dent maize, in

* 'Corn', used as a general synonym for cereal in Britain, refers exclusively to maize in North America.

which the inner soft endosperm extends to the apex of the grain and in ripening shrinks more than the surrounding hard endosperm so that the apex of the mature grain is indented. Flint and dent maizes store well and are by far the most important types grown for grain. Flour corn, in which the whole of the endosperm is soft and floury, was preferred by the American Indians on account of the ease with which it could be ground, but it stores badly and is now of negligible importance. Waxy maize is a comparatively recent development, in which the whole of the starch consists of amylopectin; this can be milled to give a starch forming a stable gel, used in the preparation of some processed foods and in the manufacture of a tapioca substitute (true tapioca is prepared from the root of cassava, *Manihot esculenta* Crantz., a tropical member of the *Euphorbiaceae*). Other mutant genes which have been used in the development of new maize types are ones increasing the proportion of lysine in the protein, and ones increasing the proportion of amylose, and decreasing that of amylopectin, in the starch.

Pop corn has very hard endosperm and the rather small usually pointed grain expands explosively on heating, turning the grain inside out to give a product which is eaten whole, without milling. Sweet corn is a very distinct form, used in the immature stage as a vegetable. Here the food reserve in the endosperm consists largely of sugar, not starch. The ripe grain, used only for seed, is consequently shrivelled in appearance.

Within each of these types of maize a large number of cultivars exist. All the older varieties were open pollinated, and therefore, since cross-pollination occurs to the extent of about 95%, somewhat variable. These have now been almost completely replaced by hybrid cultivars, which have the advantages of higher yields due to heterosis and of greater uniformity. The separate male and female inflorescences of maize make the large-scale production of hybrid seed relatively easy, two distinct lines being interplanted and the plants to be harvested for seed being detasselled, so that all pollen comes from the other line. For the hybrid to be uniform, the two parent lines must be homozygous and must therefore be closely inbred. This results in marked diminution of vigour in the parent lines, with consequent low yield of F.1 hybrid seed. It is usual therefore to employ the double cross method, using two pairs of parent lines and recrossing the two F.1s; since these are vigorous plants a high yield of double cross seed is obtained, with little loss of hybrid vigour. The mechanical removal of male inflorescences can be obviated by using a male-sterile line as seed parent, Hybrid maize varieties give a yield increase of perhaps 20% over open pollinated; their use was introduced in the U.S.A. in

the middle 1930s; by 1945 they occupied over 90% of the U.S.A. maize area, and by now have almost completely replaced open-pollinated forms in all the more advanced maize-growing areas of the world.

Maize endosperm, like all endosperm tissue, is triploid, with two sets of chromosomes derived from the seed parent and one from the pollen grain. The grain therefore shows xenia, the effect of pollen of different genotype. Thus for instance a sweet corn ear, some florets of which have been pollinated by pollen from a starchy maize, will show starchy grains mixed with the sweet ones, since the starchy character is dominant to sugary. Some degree of isolation between varieties is therefore necessary with crops for food as well as with seed crops; under normal conditions, where different varieties are not closely interplanted, this is not a serious problem.

Maize, with massive mainly single-shoot plants is grown at much wider spacing than such cereals as wheat. There may be as few as 10 000 plants per hectare from a sowing of some 10kg/ha in the southern U.S.A. 'corn belt', where varieties with a long growing season are used. Originally the ears were hand-harvested, dried on racks and later threshed; with the change to harvesting by combine there has been a move towards rather smaller ears from multi-ear plants more closely spaced. In areas with a shorter growing season, where earlier smaller cultivars are used, and available water supply is greater, closer spacings are needed. Maize shows the same type of flat-topped curve connecting yield with plant population as is found in other cereals. Thus in northern France, the early cultivar INRA 258 showed an optimum yield approaching nine tonnes per hectare at a population of 75 000 plants per hectare. At this spacing the average number of ears per plant was very slightly less than one, with an average of 125 g of grain per ear. Both ear number (about 1·5 per plant at 40 000 plants/ha) and grain per ear (145 g at that spacing) fell with increasing density, but this was more than compensated for by increased plant number up to 75 000 plants/ha; above this density the yield fell away again. The economic optimum would be about 60 000 plants/ha.

MAIZE IN BRITAIN

Grain

Britain may be regarded as being on the extreme margin of the region suitable for maize, and maize for grain is only practicable in southern England. In favourable localities, and in good years, yields in excess of those of the commoner cereals may be obtainable, but this cannot

Fig. 47. Maize; appearance of whole plants at end of August. A, tall late variety (White Horse Tooth). B, dwarf early variety (Wisconsin 240). $\times\frac{1}{30}$.

be relied upon. Only the earliest maturing cultivars are suitable; initially in the 1950s such varieties as the open-pollinated Goudster from Holland, and American hybrids such as Wisconsin 240 were employed. These have been replaced by newer hybrid cultivars derived from crosses between old low-yielding but well adapted European flint maizes, which presumably had originated from very early introductions from America, and high-yielding American dent maizes. Even with these early maturing cultivars harvest is late; grain can only be harvested by combine without damage when its moisture content has fallen to about 40%, and this stage is not usually reached until late October or November. Artificial drying is of course necessary, unless some system of wet grain storage is used.

Maize is susceptible to take-all and frit fly, but these rarely cause serious damage; the main troubles are *Fusarium* stalk rot and stem break. Cultivars with high sugar content in the stem base are more resistant to *Fusarium*. The N.I.A.B. Recommended Lists score cultivars for resistance as well as for yield and earliness.

Silage

Maize can be grown as a vegetative forage crop in Britain and this was

an occasional practice in the early part of this century. Large-growing late varieties, particularly White Horse Tooth, from the southern U.S.A., were employed; it was not expected that they would produce grain; the object was to provide leafy relatively drought-resistant forage in July and August.

This method of using maize for forage has been superseded by the growing of earlier varieties harvested for whole-crop silage in September or October. This is essentially growing for grain, but accepting that the caryopsis, although it may reach its full content of reserve food material, will not reach a stage when it is harvestable as grain. The same cultivars can be used as for grain production, or slightly later ones; the highest grain yielders are not necessarily the best for silage. Locality and weather conditions are less limiting than for grain, and maize silage is practicable over the greater part of the southern half of Britain. It is necessary however that for good silage the dry matter of the whole crop should reach 20% (25% is preferable for tower silage) before it is damaged by frost. In a normal silage crop the ears contribute some 40 to 45% of the dry weight, with a digestible dry matter content of about 80%; the remainder comes from the stem and leaves (stover), in which the DDM content is about 65%. The D-value of the whole crop should be about 70; dry matter yields of up to 16 tonnes per hectare are possible. Higher densities than for grain are used, usually from 110 000 to 150 000 plants per hectare. Although the unripe grain thus normally makes a very significant contribution to the DDM yield, it has been shown experimentally that it is not essential; plants in which pollination has been artificially prevented reach approximately the same DDM yield as those which set grain, the stover and husk leaves here acting as the food storage organs, rather than the grain.

Maize is thus of relatively limited importance as a grain crop in Britain, and the area devoted to it is unlikely to increase substantially unless forms with lower temperature requirements can be produced. As a silage crop it compares favourably in the southern half of Britain with other available forage crops. Maize is resistant to the very effective long-lasting herbicide atrazine, so that in spite of the very incomplete ground cover in the early stages of growth, weed infestation is not a problem.

Sweet corn

Sweet corn, which is a very distinct form of the maize species, is grown in southern England as a vegetable crop mainly for direct sale of the whole ears (usually referred to as cobs); a small proportion is pro-

cessed. Plants are short but multi-tillered and are grown at a wider spacing than grain maize, about 50 000 plants per hectare. Cultivars vary in length of growing season from about 100 to 150 days; ears are picked individually when the developing grain is at the correct sweet milky stage. Filling of grains is often incomplete; cobs with a 10 cm length of grains 80% filled are regarded as marketable. The current N.I.A.B. list should be consulted for information on available cultivars. Sweet corn should not be grown immediately adjoining any starchy maize in view of the danger of cross-pollination and consequent admixture of starchy grains on the sweet corn cobs.

Coix lacryma-jobi L., **Job's tears,** adlay, is another annual member of the tribe *Maydeae.* It has short inflorescences with, at the base, several female spikelets (of which one is fertile) borne inside a bead-like involucre, and above this a number of male spikelets. Grown for beads, and forms with soft involucres as a minor cereal in eastern Asia and the Philippines.

6

HERBAGE GRASSES: GENERAL

TILLER PRODUCTION AND GROWTH-HABIT

In the annual grasses all tillers are of the type described on p. 30—that is, they grow up within the sheath of the subtending leaf; their internodes remain short while they are in the vegetative condition, and do not elongate until an inflorescence is produced. Such tillers are described as *intravaginal* (within the sheath). In some perennial grasses, however, another type of tiller is produced; this grows horizontally, bursting out through the base of the leaf-sheath subtending it, and forms a spreading stem which is described as a *rhizome* if underground and a *stolon* if above-ground. In both these types of stem the internodes are more or less elongated. Such a tiller is described as *extravaginal* (outside the sheath).

The presence or absence of such extravaginal shoots, and the length to which they grow, has a marked effect on the general appearance or *growth-habit* of the plant. Grasses with all shoots intravaginal (e.g. cocksfoot, perennial ryegrass) will form dense tufts with the tillers tightly packed together and not show any great ability to spread. Those with short rhizomes (e.g. meadow foxtail) will form looser tufts and spread more rapidly to form a continuous turf, while those with long rhizomes (e.g. red fescue) or stolons (e.g. creeping bent) will form creeping plants which may spread to occupy large areas. On rhizomes, growing underground in the absence of light, the leaves are represented by scales, which usually cover only a small part of the internode; if the buds in their axils develop they grow out to form branch rhizomes. Eventually the tip of the rhizomes turns upwards and produces transitional leaves, intermediate between scale-leaves and normal foliage leaves; when it comes above ground normal foliage leaves are produced, and the newly-formed internodes remain short, so that the apex of the rhizome takes on the structure of a typical vegetative tiller. If only extravaginal shoots are produced, then such tillers will appear singly as scattered shoots separated by greater or lesser lengths of rhizome (e.g. the creeping fescue of sand dunes, *Festuca juncifolia*). Many grasses, however,

produce both kinds of shoot, and in them the apex of the rhizome, coming above ground, may produce intravaginal shoots, giving small tufts of shoots, each tuft being separated from the next by a length of rhizome (e.g. couch).

Short stolons may be formed by the slightly-elongated internodes at the base of a tuft of intravaginal tillers; these stolons gradually increase in length as the plant grows older and further internodes are added to them. Such short stolons are formed in the gradual spread of old plants of tufted grasses; if no treading takes place there may be few roots produced, so that the outer tillers of the clump merely lie on the surface of the ground, but on plants which are grazed and trampled so that the base of the tillers is pressed into the ground, numerous roots may arise, so that these gradually-lengthening stems behave as true stolons.

Longer stolons of typical creeping grasses usually arise as extravaginal shoots, with uniformly-elongated internodes. The leaves produced on such stolons are usually similar to normal foliage leaves, but are often small and with very short sheaths. Buds in their axils may grow out either intra- or extravaginally (the distinction where sheaths are short may not be very clear-cut) to form either more or less erect, leafy tillers, or branch stolons.

The majority of grasses of first-class agricultural value in this country are either tufted or with very short rhizomes or stolons. In them the bulk of the tissue produced during the vegetative period is leaf, which is not only the most valuable part of the plant for animal feeding, but is also capable of photosynthesis. Thus a large proportion of the material produced by photosynthesis is devoted to increasing the leaf area, and hence to increasing still further the amount of photosynthesis; yield, both total and useful, is therefore at a maximum in these grasses. Yields could, in theory, be still further increased by the use of herbage grasses with the photosynthetically more effecient four-carbon-atom metabolic pathway. These are however essentially tropical grasses, and it does not seem probable that species of this type can be developed for temperate use in the foreseeable future. A more promising line of possible advance would perhaps be the development of forms of temperate grasses with more erect leaves. These, while retaining the normal characteristic of three-carbon-atom pathway plants of reaching saturation at low light intensities, could give less shading of lower leaves, hence better sharing of available light amongst the leaves, and consequently greater total photosynthesis and yield. Selection for reduced respiration, and for lower rates of transpiration under dry conditions are further possibilities.

The production of long, horizontal stems implies the diversion of food material to tissue, which is not merely not photosynthetic, but which is also either inaccessible to stock or is of low feeding value. Hence in such creeping grasses both the total yield, and the proportion of it which is useful to stock, are reduced. Many grasses with far-spreading rhizomes will grow satisfactorily only in loose soil or in sand or mud; they tend therefore to be arable weeds (e.g. couch) or at best useful sand-binding plants for preventing erosion by wind or water (e.g. marram grass). The tufted grasses are, however, often less resistant to drought than rhizomatous ones and, being much less able to spread, often compete poorly with grasses with either stolons or rhizomes. It is thus essentially only in cultivated grassland, under good conditions, and in short leys, where strong, early growth is more important than later competitive spread, that these tufted grasses show to full advantage.

GENERAL PHYSIOLOGY AND AGRICULTURAL REQUIREMENTS

The method of growth of grasses makes them, in general, ideal plants for grazing or repeated cutting, in that their stems, during the vegetative period, either remain very short or creep horizontally. All stems and buds are thus at or near ground-level, and grazing or cutting removes only leaves, since these are the only parts of the plant standing above this level. The growing points of the stems, and the axillary buds, remain intact, and the production of further leaves and shoots is not interfered with. Moreover, since individual leaves increase in length by means of meristems at the bases of the leaf-sheath and of the leaf-blade, the removal of the tip of a young leaf does not prevent further growth of that leaf.

The value of a particular grass for herbage use will depend on its total annual yield (and, for long leys, on its persistence) and on the palatability and nutritive value of this yield. The yield will depend on the rate of growth of the plant and on the length of time for which this growth continues. Each individual tiller is constantly producing new leaves during the period of vegetative growth, but there is also a constant dying-off of older leaves, so that the number of living leaves per tiller does not increase indefinitely. Increase in size of the plant takes place by the production of new tillers, and during the vegetative phase the rate of growth in total size mainly depends on the rate at which new tillers are produced. Thus, in a vigorously-growing young plant of perennial ryegrass, every axillary bud produces a tiller, and the development of the bud takes place while the subtending leaf is still growing, so that the new tiller is visible above the leaf-sheath of

one leaf by the time the next leaf but one on the main shoot has emerged. These axillary tillers similarly commence tillering at once, so that the total number of tillers increases geometrically.

In slower- growing species, only a small proportion of the axillary buds develop, so that the rate of tiller production is very much lower; this is particularly marked where rhizomes or stolons are produced and food material thus diverted to the production of non-photosynthetic structures. Even in the very rapidly-growing grasses like perennial ryegrass, the rate of increase in tiller number tends to fall off as conditions become less favourable. Reduction in light owing to the shading effect of the crowded tillers is an important factor in this; tillering rate being lower at lower light intensity. Tillering rate falls off rapidly with the onset of winter; this falling-off of tillering is, in perennial ryegrass, greater than the falling-off in leaf production, so that leaves are formed with no axillary tillers. When new tillers begin to arise again in spring, they are formed in the axils of newly-produced spring leaves, and not by development of dormant buds in the axils of over-wintered leaves. The date of the beginning of vigorous growth in spring is partly a character of the particular grass; thus in general perennial ryegrass and cocksfoot are species which start growth early, while timothy and bent are late, but there is considerable difference between different plants of the same species (see below, p. 139). It is also partly controlled by previous treatment; thus, in cocksfoot entering the winter grazed down hard, and hence with little stored food reserves, growth starts later in spring than when the plant has been allowed to grow and build up reserves in the previous autumn.

Behaviour of the grass plant during late spring and summer is largely a matter of the change from the vegetative to the flowering condition. When an individual tiller changes to the flowering state, not only does production of further leaves stop, but development of buds in the axils of leaves already initiated also stops. In the great majority of grasses of temperate regions, the change to the flowering condition is a response to increasing length of day, but tillers must have reached a certain minimum age and size before they can respond in this way; a tiller which has reached this stage can be described as 'ripe to flower'. If a grass requires a very short period to become ripe to flower, then, once the daylength is sufficient for that particular plant, all tillers formed will reach this stage before the day-length decreases again. In this case, the plant will behave as an annual, all tillers flowering and dying off after producing seed, or, if they become ripe to flower while still very small, dying without being able to produce seed. If, however, the period required is longer, then only

Fig. 48. Life-cycle of a perennial grass (perennial ryegrass). A, 'seed'. B, C, stages in germination. Tillering then takes place; a single tiller is shown at D. An individual tiller may either become fertile, developing as in F, or may remain in the vegetative condition, producing further tillers, as in E, and not reach F until later in the year, or the following year. Plants in which a large proportion of the tillers follow the direct path from D to F will be stemmy and short-lived, while those in which the majority of tillers go through stage E will be leafy and long-lived. Further development of the fertile tiller is shown in G, emergence of inflorescence, and H, mature inflorescence, which produces 'seed', A, and dies. Not to scale.

the larger and older tillers will flower, and some will remain as 'barren' tillers, which produce more new tillers before they themselves flower. If the period is sufficiently long, or if a period of exposure to cold is needed to cause flower initiation, then only tillers produced in the previous year will flower, and there will be only one flowering period per year, as in the extreme pasture forms of perennial ryegrass. If rather shorter, tillers not ripe to flower at the normal first flowering period in early summer may reach this stage in the late summer, giving a second, 'aftermath' flowering. In general, the longer the period of active vegetative growth before the flowering stage is reached, the higher will be the yield, and the greater the proportion of vegetative to flowering tillers, and consequently, since perennation depends on overwintering vegetative tillers, the longer the total life of the plant.

When growth begins the growth rate is low, since the area of leaf is small, and the amount of photosynthesis is therefore small. As growth continues the area of leaf increases, and with it the amount of photosynthesis and the rate of growth. A maximum rate of growth is reached when the leaf area index (LAI) is at its optimum, which may be, depending on the particular grass and on the conditions prevailing, in the neighbourhood of LAI 5. As more leaves are produced, the lower leaves begin to be shaded by the upper ones and their photosynthesis is therefore reduced; the rate of growth thus begins to diminish. With continued growth, a point is reached, at perhaps about LAI 10, where the dying-off of heavily-shaded lower leaves balances out the production of new leaves. This is the ceiling LAI; there may be some small increase in the non-photosynthetic parts of the plants after this point, but the ceiling yield is soon reached. If the crop is left beyond this period, there is no further increase in yield.

These changes in the rate of growth mean that the total yield of a grass sward will be very much affected by the way in which it is treated. If it is cut frequently (or grazed hard, which will have approximately the same effect), so that the optimum LAI is never reached, the total annual yield will be low. With less frequent cutting, or laxer grazing, the yield will increase, but since above the optimum LAI the rate of growth decreases, excessively long periods between cuts will result in the total annual yield falling again. Total yield of dry matter is, however, not the only point to be considered; the grass is grown for feeding to animals, and it is that part of the dry matter which can be utilized by the animals which is important. Young grass consists largely of meristematic tissue and parenchyma, with only a small proportion of lignified tissue. Its D-value, that is to say the percentage of its dry matter which consists of digestible organic matter, is therefore high, and, since the proportion of cell contents in such tissue is high, the amount of protein in this digestible organic matter is also high. Older growth has a higher proportion of lignified tissue, and its D-value is lower. Consequently the yield of digestible organic dry matter (DODM) does not rise as rapidly as the yield of total dry matter with increasing age of grass. Infrequent cutting, or long rest periods between grazings, gives the highest total annual dry matter production, but at the expense of quality; frequent cutting or grazing gives a high quality product, but the yield is low. The highest production of DODM per annum is obtained by a treatment intermediate between these two extremes; this will usually be defoliation at intervals of something like four to six weeks, depending on the type of herbage and on the conditions.

The D-value of the herbage is affected by factors other than fre-

quency of defoliation. One of these is stage of growth. The effect of this is particularly marked in the primary growth in spring and early summer, when many tillers are changing from the vegetative to the flowering stage. This change involves the relatively rapid production of elongated stems. Young stems consist largely of parenchyma and have a D-value comparable to that of leaves, but in older stems lignification takes place and, since lignin is not digestible, their D-value is lower. There is thus a progressive fall in the overall D-value of the herbage during inflorescence production. The timing of this fall in relation to inflorescence emergence varies in different species and in different cultivars of the same species. Thus the

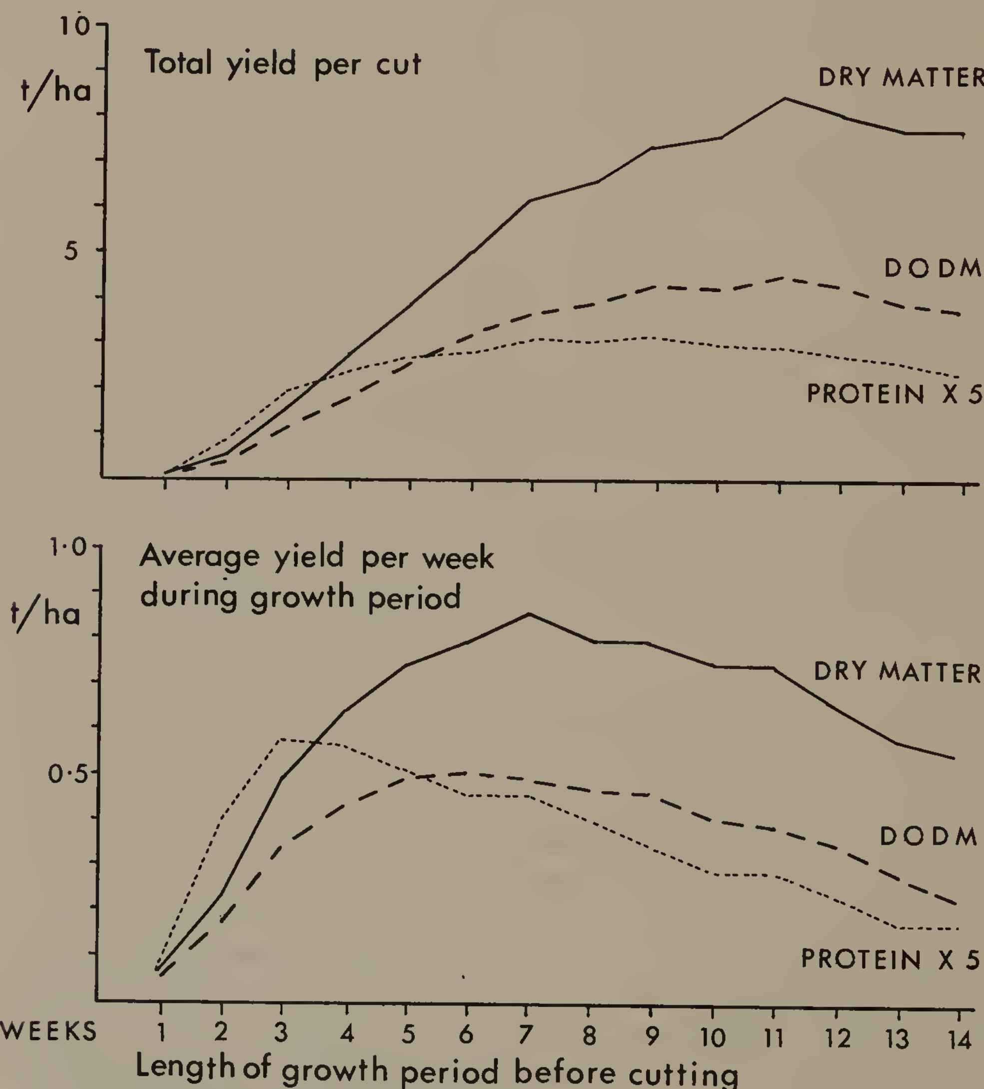


Fig. 49. Production of dry matter, digestible organic dry matter (DODM) and protein during primary growth of S. 22 Italian ryegrass. Figures are means of results for three different years and for four nitrogen levels. Data from Wilman, D., *J. Brit. Grassld. Soc.*, **30**, 1975.

D-value has fallen from an initial figure of about 70 to a value of 63 two weeks after inflorescence emergence in early cultivars of perennial ryegrass, but to the same figure in late cultivars at the time of ear emergence. In timothy, on the other hand, the D-value of early cultivars has fallen to 63 two weeks before ear emergence, and that of late cultivars four weeks before this growth stage is reached.

The D-value of herbage may also be affected by time of year, even when the production of flowering stems is not involved. Thus the D-value of four-weeks-old regrowth of perennial ryegrass in spring may be as high as72, but may fall to 66 in summer, and rise again to 70 in autumn.

The D-value of a grass at a particular stage, and hence its feeding value, will be influenced not only by the proportion of leaf to stem, but also very much by the structure of the leaf. The leaf-blade is normally of higher value than the sheath, but very marked differences exist between the leaf-blades of different grass species. The general structure of the leaf-blade has already been described (p. 33); while the structure of the vascular bundles is rather similiar in all species, and the amount of xylem always small, the extent to which sclerenchyma develops as strengthening tissue above and below the bundles varies very much, and has a profound effect both on the nutritive value and the palatability. Thus in a palatable grass of relatively high value, like rough-stalked meadow-grass, sclerenchyma is present only as very

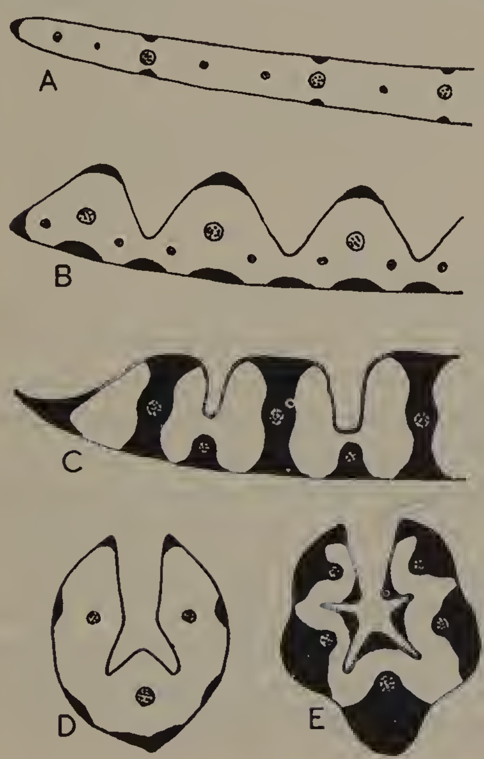


Fig. 50. Diagrams of transverse sections of grass leaf-blades to show varying amounts of sclerenchyma. A, rough-stalked meadow-grass. B, tussock grass. C, marram. D, sheep's fescue. E, *Nardus*. Schlerenchyma black; vascular bundles stippled.

slender strands adjoining the epidermis above and below the main vascular bundles, and along the margins. In an unpalatable grass, such as tussock grass, which is usually avoided by stock, stout and closely-spaced sclerenchyma strands develop on the lower side, together with other strands capping the ridges and edging the margins. In a completely inedible grass, such as sea lyme-grass, which is of value only as a sandbinder, the main vascular bundles are embedded in a stout 'girder' of sclerenchyma, extending the whole way from the lower to the upper epidermis. The same trend can be seen in the grasses with permanently-folded, bristle-like leaves; thus in the relatively palatable sheep's fescue forms there is a comparatively small sclerenchyma strand outside each main bundle, whereas in the similarly-shaped but very unpalatable leaf of mat-grass (*Nardus*) at least a third of the whole cross-sectional area is occupied by sclerenchyma.

Palatability is reduced by hairiness and by bitter-tasting substances as well as by high fibre content. Thus Yorkshire fog shows by chemical analysis a relatively high feeding value, and has a D-value only some five units below that of perennial ryegrass at the same stage, but it is unpalatable, partly owing to its excessive hairiness, and this grass is little grazed by stock, except under extreme conditions. Palatability is also affected by the soluble carbohydrate content of the grass. If two herbages have the same D-value, the one that has the greater soluble carbohydrate content will generally be more palatable, and thus usually give a higher voluntary intake by animals, and hence a higher animal production. Soluble carbohydrate content may differ between different cultivars and between different stages of growth; it is also affected by physiological conditions, being depressed by wet weather and by high nitrogen.

GRASS CULTIVARS

Plants belonging to the same grass species will all have the same general structure of inflorescence and vegetative parts, but may show considerable variation in physiological and quantitative characters. Thus we may find plants which, while they are all clearly recognizable as belonging to one species, differ in size, rate of tillering, length of vegetative period, proportion of fertile tillers, time of flowering, winter-greenness, disease-resistance and other characters which considerably affect their agricultural value. The great majority of grasses used for herbage are grown from seed produced as a result of cross-pollination, and variation from plant to plant always occurs. It is not practicable to build up a stock of identical or nearly identical plants,

as it is with a vegetatively-propagated plant such as potato, or with a self-pollinated plant such as wheat. The most that can be done on an economic scale is to develop a series of plants, which, although not identical, are all somewhat similar, and show much less than the total range of variation found in the species as a whole. Such a group of plants, varying within more or less narrow limits, is described as a variety or cultivar of the particular species.

Any naturally-occurring population of grass plants of a single species will have been subjected to a natural selection, so that it will consist only of types suited to the particular local conditions prevailing. (Such types selected by natural ecological conditions are known as *ecotypes*.) Thus in Britain, where most grassland is only maintained as such by the influence of grazing animals preventing the establishment of trees and shrubs, the types found in any area of old grassland will be those which withstand grazing best, as well as being suited to the prevailing climate and soil. In addition, since establishment by natural re-seeding is not usually easy under hard grazing, they will be mainly long-lived perennial forms if the grazing has been close, any short-lived plants which may have been present originally having died out.

The old practice of allowing arable land to 'tumble down' to grass was slow and inefficient, but it did mean that the plants which established were derived from wind-borne seed from well adapted plants in neighbouring grass fields. The eighteenth century use of hand-collected seed, also from wild plants, gave much the same effect. This however was soon replaced by the much cheaper method of harvesting seed from fields specially laid up for the purpose. Harvesting for seed was most conveniently done in the first year of a ley, and hence short-lived heavy seeding plants tended to be favoured. This process of using first-year seed, repeated generation after generation, resulted in a marked shift of type within the species. What may be called commercial varieties, produced in this way, with unintentional but none the less effective selection for high seed yield rather than for grazing merit, were for a long time the only forms of the main grass species available on the market. It was not until the pioneer work of Stapledon and his colleagues at Aberystwyth in the 1920s that it was appreciated that these commercial varieties were very far from being the best forms of the species.

The use of local varieties was an improvement; here seed was obtained from good old pastures, in which the natural selective effects of good management over many years had resulted in the preservation of the best adapted and longest lived plants. Their seed yield was low, and, since an old pasture would rarely be a pure stand

of a single species, the seed was likely to be contaminated with seed of other plants. It was therefore necessary to clean it and to multiply it under ley conditions before it could be economically marketed. This multiplication was however not continued for more than a few generations, so that the adverse effects of repeated multiplication were avoided.

The majority of herbage grass cultivars now in use are bred varieties. These, produced first at Aberystwyth and later by plant breeders all over the world, represent a further improvement. In them the initial selection is the result not of the slow and relatively uncontrolled effects of local conditions and agricultural management, but of conscious choice and testing by the plant breeder. A much wider range of bred varieties within the species is thus possible, each designed to fulfil some particular agricultural purpose. Again, as with local varieties, multiplication is carefully controlled, so that the seed marketed is never more than a few generations away from the original selected parent plants.

Since almost all herbage grasses are necessarily cross-pollinated, each cultivar consists of a range of different genotypes. The range within one cultivar is much smaller than that of the whole species, but is great enough to mean that grass cultivars cannot be distinguished by simple inspection of particular morphological characters, as is possible with self-pollinating cereals. Differences are usually quantitative rather than qualitative, and comparisons, which must necessarily be statistically controlled, have to be of mean figures for a number of plants. In the tests for distinctness, uniformity and stability, which are required before a grass cultivar can be inscribed on the national list and hence permitted to be marketed, the British testing authority records figures for some fourteen or more characters on sixty plants of the cultivar. For a cultivar to be accepted as distinct, the mean value for at least one of these characters must show a difference, statistically significant at the 1% level, from all other cultivars. The characters measured are ones such as date of ear emergence, length of leaf, and others which are relatively little affected by conditions; separate tests are used to assess agricultural merit.

Identification of herbage grass cultivars in the field is thus usually possible only where some very marked difference is present. Their separation in the seed (diaspore) stage is normally quite impossible, but certification ensures that the seed as sold is true to variety.

Range of cultivars available

The total range of variation within a single grass species is often very

large, and it would theoretically be possible to produce a large number of cultivars within any species. Clearly, however, cultivars will only be worth producing if the grass is commonly sown, and the number of cultivars available is usually roughly proportional to the agricultural merit of the species, or in some cases, to its importance for sports turf and amenity purposes. Where a species has a wide geographical range it will include forms adapted to different climates, and only some of its cultivars may be suitable for use in a particular area. Thus, in general, the cultivars suitable for growing in Britain are those developed in areas with approximately similar climates. Cultivars from north-western Europe or from New Zealand, in addition to those originating in Britain, are usually satisfactory. Cultivars from areas with more extreme winters have a short growing season, and therefore a low total yield, while those from milder climates, although they have a long growing season, are not reliably winter hardy.

Cultivars will represent only a proportion of the total range of variation within a species, since on the one hand low-yielding or very stemmy or short-lived forms will usually be avoided as having little agricultural value, while on the other hand very leafy rarely-flowering forms may have to be excluded, in spite of their potentially high merit as grazing plants, because their very low seed yield would make them uneconomic to produce. Successful cultivars of a particular species will all represent forms of the species which combine high vegetative yield with at least reasonable seed yield. They will differ in date of flowering and in ratio of flowering to vegetative tillers, in distribution of growth throughout the year, in palatability and digestibility at different stages, in reaction to different methods of management and to different environmental conditions, and in disease resistance. Comparison of three cultivars of perennial ryegrass will illustrate the sort of difference which can exist. The three taken as examples are Northern Irish Commercial, representing the type of commercial variety which has now been superseded, Aberystwyth S 24 and Aberystwyth S 23. These latter two were amongst the earliest bred cultivars to be produced; S 24 is an early-flowering cultivar, originally described as a hay variety, and S 23 a late-flowering pasture variety. The figures in Table 2 are means for sixty plants of each cultivar, grown as widely spaced plants sown in late summer and recorded the following year.

The very marked differences in size of spaced plants and numbers of tillers illustrates the kind of variation which can occur between different cultivars. They are not however measures of yield under any normal grassland management system; for example, under a nine-cut

Table 2. Comparison of spaced plants of three cultivars of perennial ryegrass

	Date of start of ear emergence	Fresh weight (g) 5 weeks later, single plant	Total tillers	Ratio of vegetative to flowering tillers
Irish	2 May	660	800	0.4
S24	5 May	890	1 100	1·4
S23	6 June	1 270	2 100	1·9

system the total annual dry matter yields of S 24 and S 23 grown as normal swards differ by only two per cent.

The number of grass species considered worth sowing in Britain is small, but the number of available cultivars of these few species is very large; the N.I.A.B. Classified List of Herbage Varieties for 1977/8 records a total of 231 grass cultivars. New cultivars are constantly being produced, and the current Classified List should be consulted. More detailed information is given in the N.I.A.B. Farmers Leaflet No. 16, *Recommended Varieties of Grasses*; this covers only those cultivars which have given good results in trials. Here again, the current leaflet should be consulted for up-to-date information.

7

HERBAGE GRASSES: SPECIAL

In the following section all the grass species which occur at all commonly in Britain are discussed individually in systematic order. The amount of detail given is in general roughly proportional to the agricultural importance of the species. For the characters and arrangement of the tribes reference should be made to the section on classification, pp. 39–42; for vegetative identification of common species see pp. 199–204.

FESTUCEAE

LOLIUM. THE RYEGRASSES

The genus *Lolium* has the typical spikelet of the tribe *Festuceae*—that is, a many-flowered spikelet not completely enclosed by glumes; but it differs from other members of the tribe in that the spikelets are borne on a spike instead of a panicle. The spike, however, is differently arranged from that of wheat and other similar plants of the tribe *Hordeae*. In them the spikelet has its flat side towards the rachis, but in *Lolium* it is placed edgewise-on to the rachis. If two glumes were present in this type of spike, one of them would lie against the rachis; in fact, in *Lolium* only one glume (the upper) is present on the majority of spikelets, and the internodes of the rachis are slightly hollowed out and may be considered to take over the protective function of the other glume. The terminal spikelet, at the apex of the spike, has the usual two glumes.

The inflorescence thus consists of a spike, with a variable number (usually from twelve to twenty) of spikelets placed singly at the nodes of the rachis, and edgewise-on to it. Each spikelet consists of one rather narrow boat-shaped glume, and some six to twenty florets, each with a usually five-nerved lemma, rounded on the back, and with or without a terminal awn.

The common name 'ryegrass' is not particularly appropriate, as there is no very close resemblance or relationship to rye (p. 80); it is,

in fact, a corruption of the earlier name 'ray grass', itself derived from the old French name, *ivrai* (*ivre* = intoxicated), applied to the poisonous species, *Lolium temulentum,* darnel, on account of the symptoms it produces. The name then came to be extended to cover all the species; 'eaver', a local name in south-west England, is derived from the same source.

The genus contains some six species, of which two, perennial and Italian ryegrasses, are of outstanding importance in British agriculture and together account for some 67% of the total grass seed used in Britain. The two species cross readily to produce fertile offspring, and are therefore treated by some botanists as subspecies (*Lolium perenne* L. subsp. *perenne* and subsp. *multiflorum* (Lam.) Husnot). In view of their agricultural distinctness they are here treated as separate species.

Lolium perenne L. **Perennial Ryegrass**

A native perennial, extremely common and of great agricultural value.

Inflorescence. In *L. perenne* the glumes are short, usually not more than half the length of the whole spikelet, and the lemmas end in a rather blunt point, with no awn. The spikelets usually have some six to twelve florets.

'Seed'. On threshing, the rachilla breaks up, and the 'agricultural seed' consists of the caryopsis, which may be purple in colour, enclosed within the pale brown lemma and somewhat transparent palea. The rachilla is flattened and widens gradually from below upwards (cf. meadow fescue, p. 150). The length is usually 4–6 mm, about 550 000 per kg.

Vegetative characters. The whole plant is perennial, tufted in growth and with intravaginal tillers only. All parts are glabrous. The leaves are folded in the bud, giving distinctly flattened vegetative shoots. The expanded leaf-blade is tapering, rather narrow; it is ribbed, dark-green and dull on the upper surface; keeled, lighter green and very shiny on the lower surface. Auricles are present, but these are small and often reduced on the leaves of vegetative tillers to mere ledge-like projections. The ligule is blunt and very short. The leaf-sheaths are split (not quite to the base), shiny, with a bright, cherry-red coloration at the base (a form without red colour exists, and was at one time available under the name of 'golden ryegrass'. It

is, however, uncommon; it is a double recessive for the two genes controlling anthocyanin production). The leaves develop little sclerenchyma, and the old leaf-sheaths are not persistent, but rot away comparatively quickly (for illustration see p. 199).

Agricultural importance. Perennial ryegrass is very common, and perhaps the most important of all grasses in British agriculture. It is palatable, stands up to hard grazing well, and under conditions of high fertility gives high yields of leafy herbage. It is winter-green, commencing growth early in spring and continuing well into autumn. During primary growth in spring dry matter may be accumulated at a rate of over 100 kg/ha per day. Digestibility falls off comparatively slowly during primary growth and a dry matter yield of 5 000 kg/ha may be reached by the time the D-value falls to 67. During regrowth after cutting the digestibility again falls relatively slowly, and 67 D is reached in about six weeks. Total annual dry matter yields of about 11 000 kg/ha may be obtained under good conditions and some 300 kg/ha nitrogen with a nine cut regime, or about 15 000 kg with four cuts. Perennial ryegrass is however not a grass for poor conditions or low fertility, and is not drought resistant. Where nitrogen and water are limiting yields are much reduced; with 60 kg/ha nitrogen and no clover present an annual yield of only 3 000 kg/ha has been recorded. While the total growing season is long, the main flush of growth occurs around May, and this period of maximum growth is not readily altered by management methods. It may be possible by selection of different cultivars within the species, and by varying the time of nitrogen application, to arrange to shift this flush of growth perhaps a month, but it is not usually possible to arrange for it to be produced at other times, or to avoid a depression of yield in the middle of the season. For good, fertile lowland conditions, however, perennial ryegrass is usually the most generally useful species, and forms the basis of most leys and pastures under such conditions. Its comparatively cheap seed and ready establishment make it suitable for short leys, and as a result a greater tonnage of perennial ryegrass seed is used annually than of any other grass.

Owing to its large seed and the rapid growth of the seedling, perennial ryegrass establishes well, under good conditions the field establishment may be 60% or more (see p. 211). Its rapid early growth may cause difficulty when it is sown with other grasses, the ryegrass being very *aggressive* and tending to compete so strongly with other slower-growing grasses that they are at least partially suppressed. General purpose multi-species seeds mixtures based on perennial ryegrass are however quite practicable (see p. 214) and are

in fact extremely popular. Perennial ryegrass is thus the basis of the great majority of the medium and long term leys sown in Britain, as also of all the better old pastures (see p. 206), where indeed the perennial ryegrass content can be regarded as an index of quality. Furthermore, perennial ryegrass is a valuable amenity grass for all but the finest lawns, attractive in appearance and standing up well to hard wear when used in sports turf. It is thus unquestionably the most important of all the perennial grasses grown in Britain.

Cultivars

Perennial ryegrass is a variable species and crossing may take place not only between different forms of the same species, but also with Italian ryegrass and with some species of fescue. Very short-lived and sparsely tillered or very low-yielding forms are of little agricultural value, but even if these are excluded, the range of variation is still large. Apart from the extensive range of varying genotypes present in old grassland throughout Britain, some 85 different and distinguishable cultivars are included in the United Kingdom national list (1978). These are mainly cultivars bred here or in other parts of north-western Europe, but the list includes a few local varieties.

Cultivars are most conveniently grouped according to their time of flowering. An almost continuous series exists, from early cultivars with 50% of their inflorescences emerged before mid-May in central England, to extra-late cultivars not reaching this stage until after mid-June. Generally speaking early-flowering forms tend to start growth earlier in the year, with early cultivars producing some 20% of their annual yield by 1st May, and giving a first conservation cut at about 63 D-value in the last week of May, while late and very late cultivars give only some 10–14% by 1st May, and can be cut at 63 D up to the end of June. In most of the late cultivars the fall in digestibility is more rapid than in the earlies, so that the difference between cutting dates at the same D-value for earlies and lates tends to be less than the difference in heading dates. There is no consistent difference in total annual yields. In general, later cultivars tend to be more prostrate, more persistent and less competitive as young plants but more competitive in later years.

Cutting across these differences are those associated with chromosome number. The typical perennial ryegrass is a diploid with fourteen chromosomes, but a number of auto-tetraploid cultivars with twenty-eight chromosomes are available (16 out of the 85 listed). These vary from early to late, and their general growth pattern is similar to that of diploids of the same heading date. They have

however larger cells, and thus a higher ratio of cell contents to cell wall; their soluble carbohydrate and water content is higher than in diploids, and their digestibility and palatability higher at a corresponding stage. Increased cell size means that individual plant parts are larger. Yield is not increased; there are fewer larger tillers, which results in tetraploids being somewhat less competitive, perhaps easier to manage in mixture with other species, but generally less persistent. The increase in size of plant parts extends to the 'seed' (diaspore), which is almost twice as large as that of diploids, necessitating a higher seed rate. Fertility, and hence seed yield, is usually lower than in diploids, so that seed tends to be more expensive; this, combined with the higher seed rate, makes tetraploids more costly to use. For hay or wilted silage their higher water content may necessitate longer drying times.

Tetraploids have an economic advantage only if their increased palatability results in an increased intake by animals which is more than sufficient to offset the increased water content of the fresh herbage. The evidence is that this does take place, but the advantage is not large, and tetraploids, although a very useful addition to the range of cultivars available, appear unlikely to supersede diploids.

From the 1940s onward the formerly dominant Irish Commercial perennial ryegrass was progressively replaced by local and bred cultivars. Amongst the former may be instanced the early Devon Eaver, which has given better results in some grazing trials than in the normal cutting trials, and the later Kent Indigenous, derived from old pastures in the Romney Marsh area. The bred cultivars were initially all Aberystwyth productions; these were later joined by many from the Netherlands. Amongst early and medium early cultivars Aberystwyth S 24 remained important in the 1970s, together with the somewhat higher-yielding Cropper and the very persistent Monta and the tetraploid Reveille. In the medium-late group, Aberystwyth S 101 and the later-developed not very winter-hardy S 321 tended to be replaced by the very persistent Talbot, and by tetraploids such as Taptoe. Amongst late cultivars, Aberystwyth S 23, long established as an outstanding and persistent variety for long leys, remained popular, but was challenged by a number of more winter-hardy Netherlands varieties such as Caprice and Semperweide and by the slightly later Belgian Melle, which shows high yield response to very high nitrogen levels. Fortis and Petra were available as tetraploids. New very late cultivars such as Endura, flowering one week after S 23, but retaining high digestibility ten days longer, extended the range of cutting dates for the species still further. Five cultivars for amenity purposes only were listed in 1978.

Fig. 51. Ryegrasses. 1, inflorescence, $\times\frac{1}{2}$. 2, single spikelet, $\times 3$. 3, 'seed', $\times 10$, of A, perennial ryegrass; B, Italian ryegrass; C, darnel (awned form of darnel shown in 1 and 3, awnless in 2); R, rachis; G, glume; L, lemma; P, palea; RA, rachilla.

Lolium multiflorum Lam. (*L. italicum* A. Br.). **Italian Ryegrass**

An important introduced species, behaving as an annual or short-lived perennial. (The name *L. italicum*, or *L. multiflorum* var. *italicum* Beck., is sometimes used for the commonly grown two- or three-year plant, the type of the species *L. multiflorum* being the strictly annual form Westerwolds ryegrass; this is not the E.E.C. usage, for which see p. 149.)

Inflorescence. The inflorescence closely resembles that of perennial ryegrass, but there are normally more (sixteen to eighteen) florets per spikelet, and the lemmas bear a long, fine terminal awn.

'*Seed*'. The threshed 'seed' is very similar to that of perennial ryegrass, but easily distinguished by the awn. This awn is not usually lost in the threshing or cleaning processes; if it is, then seeds can only be distinguished by the *Hellbo test*, the examination of the intermediate nerves of the lemma for minute teeth, present in Italian but absent from most forms of perennial, or by the *Gentner test*, which depends on the fact that roots of Italian ryegrass germinated on filter paper fluoresce under ultraviolet light, while seedlings of perennial (except for a small proportion in the early strains) show no fluorescence. The 'seed' is often slightly larger than that of perennial, with some 500 000 per kg for diploids, but this difference is by no means constant.

Vegetative characters. Italian resembles perennial ryegrass, but has usually larger tillers, with broader leaves. The plant is usually more erect, with a tendency to produce tillers at nodes well above ground-level. Young leaves are rolled, not folded as in perennial, so that shoots are round, not flat. Auricles are large, well-developed, long and clasping around the sheath.

Italian ryegrass can usually be distinguished from meadow fescue (p. 151) by its more succulent, quickly-grown appearance and by its less-persistent old leaf-sheaths, but plants may be encountered in which these characters are not clearly visible; it is then necessary to depend on very small details. The shape of unexpanded tiller buds (really the outline of the young prophyll) exposed by stripping down the older leaf-sheaths provides a clear distinction; in Italian ryegrass the bud is narrow, pointed and with ciliate margin, while in meadow fescue it is broad, rounded and glabrous (see illustrated key p. 201).

Italian ryegrass is not known in a wild state, and appears to have originated in cultivation in N. Italy. It was introduced into Britain in the early nineteenth century.

Agricultural importance. Italian ryegrass is probably the quickest-growing and highest-yielding of all temperate climate grasses under high fertility conditions, yielding some 17 000 kg/ha dry matter under good conditions compared with perhaps 15 000 for perennial ryegrass. It is therefore of outstanding importance in short leys, where its lack of permanence is not a disadvantage. It establishes readily and grows very rapidly, so that it may be fit to graze within a few weeks of sowing and is generally amongst the most palatable of all grasses. It starts growth in the spring earlier even than the early perennial ryegrasses but flowers about a week later than these, so that the period of vegetative growth is longer. It is not only higher yielding than perennial ryegrass, but more adaptable, in that it lends itself more readily to treatments designed to prolong the grazing period, and by selecting suitable times of sowing and methods of management, keep can be obtained from Italian ryegrass at almost any desired time of year. Under good conditions a system of intensively managed short leys based on Italian ryegrass can give higher yields than any other grassland system.

Italian ryegrass was formerly used in considerable quantities as a constituent of three-year and longer leys; its exceedingly vigorous and aggressive early growth may make this a dangerous practice, as, unless very carefully managed, it competes too strongly with other slower growing grasses. Mixtures with the only slightly less aggressive perennial ryegrass are usually satisfactory.

Range of forms

The species *Lolium multiflorum* includes annual forms as well as the typical Italian ryegrasses. The hybrids with perennial ryegrass can also be conveniently considered here, as resembling Italian in characters and uses. Tetraploids show the same sort of difference from diploids as those described for perennial ryegrass. The total range of available forms is as follows:

Hybrid Ryegrasses (*Lolium* × *hybridum* Hausskn.).

Casual hybrids between Italian and perennial ryegrasses have usually little merit, and satisfactory isolation between seed crops of the two species is essential. A number of cultivars have however been bred which combine the high yield and palatability of Italian with increased life span derived from perennial; for two-year leys these may be better than the shorter-lived Italian. Grasslands Manawa is a diploid, persistent for two years or slightly more, flowering with the

true Italians; it has the disadvantage, shared with some other cultivars of New Zealand origin, that it is not reliably winter-hardy. Sabrina and Sabel are tetraploid hybrids heading at the same time as the early perennials, more persistent than the true Italians, and satisfactorily winter-hardy. Six cultivars of hybrid ryegrass were listed in 1978/9, including four tetraploids.

Italian Ryegrass Proper (*L. multiflorum* subsp. *non-alternativum* in E.E.C. usage).

These are biennials or short-lived perennials, not normally flowering in the year of sowing. The Irish Commercial mainly used in the early part of the century was superseded by the more leafy Aberystwyth S 22, and this in turn by a number of continental diploid cultivars, including the Belgian R v P, high-yielding but with rather low digestibility of regrowth. Sabalan from Aberystwyth shows the typical tetraploid characters combined with resistance to mildew and other foliar diseases. In 1978/9 a total of 19 diploid and 13 tetraploid cultivars were listed.

Westerwolds Ryegrass (*L. multiflorum* subsp. *alternativum* in E.E.C. classification).

The strictly annual form of *L. multiflorum* is used where maximum production is required within six months of sowing; Westerwolds ryegrass is thus primarily a grass for catch-crop or green manuring leys. When sown in spring or summer it flowers in the same year. It originated in the Netherlands; Dutch Westerwolds (a maintained stock derived from the original Dutch Commercial) is available as well as diploid and tetraploid bred cultivars. Differences between diploids and tetraploids are less marked than in other ryegrasses; 9 diploid and 4 tetraploid cultivars were listed in 1978/9.

***Lolium temulentum* L. Darnel**

Darnel is a strictly annual, southern European species, very similar in the vegetative stage to a sparsely-tillered plant of Italian ryegrass, with rather rougher leaves. It is readily distinguished when in flower by the greater length of the glumes, which extend beyond the top of the uppermost floret of the spikelet. The florets are considerably broader than those of Italian; the lemma may be awnless (var. *arvense* Lilj.) or bear a fine terminal awn.

Darnel is valueless as a herbage grass, but was formerly important

as a weed of cereal crops. The 'seed' (caryopsis enclosed in lemma and palea) is much larger than that of the other ryegrasses; and sufficiently near to a wheat grain in size and shape for it not to be separated by primitive cleaning methods. The seed may be poisonous, owing to the presence of a sterile fungus mycelium, and wheat contaminated with darnel was therefore dangerous to use for food. Improved methods of seed-cleaning have reduced the importance of darnel to negligible proportions in Britain, where it is now a rare plant. It is however still a serious weed in some countries, and as an impurity of cereal seed samples is subject to the same stringent regulations as wild oats (see p. 101).

Lolium remotum Schrank. is a small annual with narrow spikelets and slightly swollen lemmas; it does not occur in Britain except perhaps as a rare casual, but may be an important weed of linseed or flax in some areas and is therefore subject to special rules under the 1976 regulations for oil and fibre plant seeds.

FESTUCA. THE FESCUES

The genus *Festuca* is closely related to *Lolium*, and crosses are possible between many species of the two genera. It is distinguished by the inflorescence being a panicle, not a spike; all spikelets have two glumes. The members of the genus are all perennials, annual species being placed in the genus *Vulpia*. (The bromes, genus *Bromus*, have panicles resembling fescues in general appearance, but are distinguished by the hairy ovary with enlarged tip, and by the dorsal, not terminal, awns on the lemmas.)

The species of *Festuca* of agricultural importance fall into two groups: (1) the large fescues, with all leaves broad and flat—meadow and tall fescue; and (2) the small fescues, with permanently-folded, bristle-like leaves—sheep's fescue and related species.

Festuca pratensis Huds. (*F. elatior* var. *pratensis* (Huds.) Hack.). **Meadow Fescue**

A tufted perennial, palatable and of considerable value in leys.

Inflorescence. A spreading panicle 60–90 cm high; panicle branches usually in pairs, unequal, some with only one to two spikelets. Spikelets cylindrical, six- to twelve-flowered.

'Seed'. Caryopsis enclosed in palea and blunt, awnless, round-backed lemma. Very similar in size and shape to perennial ryegrass,

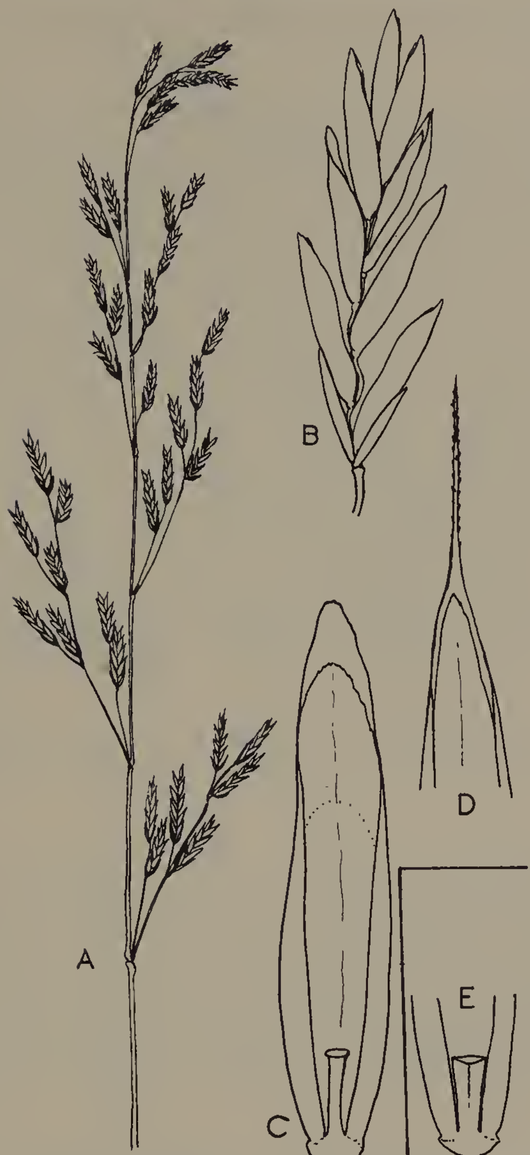


Fig. 52. Meadow fescue. A, panicle, $\times\frac{1}{2}$. B, spikelet, $\times 3$. C, 'seed' $\times 10$. D, apex only of 'seed' of tall fescue for comparison with C. E, base only of 'seed' of perennial ryegrass for comparison of rachilla.

but distinguished by cylindrical (not flattened) rachilla, widening abruptly at top.

Vegetative characters. Tufted perennial, tillers intravaginal. Leaves rolled in bud, shoot round, glabrous. Leaf blades broad, tapering ribbed, dull above, shiny below. Upper surface of blade slightly rough. Auricles conspicuous, glabrous, ligule short. Sheaths split, shining, bright cherry-red at base. Very similar to Italian ryegrass, distinguishable usually by harder, less succulent, slower-grown

appearance, and persistent pale-brown old sheaths. (For distinction by bud-shape, see Italian ryegrass, p. 147, and illustration p. 201.)

Agricultural importance. Meadow fescue is a useful herbage grass for longer leys, palatable, high-yielding and winter-green. Growth in the seedling and young plant stages is rather slow, and meadow fescue suffers very badly in competition with the ryegrasses. Its inclusion in general-purpose leys based on ryegrass is therefore not to be recommended. It has, however, advantages over perennial ryegrass for some purposes as being more flexible in its reactions to varied management, and capable of providing keep during the winter and midsummer periods, when ryegrass yield is low. Once established it is more resistant to drought and to waterlogging than perennial ryegrass, more winter-hardy and more tolerant of slightly lowered fertility. Yields are however rather lower, totalling some 10 000 kg/ha dry matter under a nine-cut system and some 12 000 with four cuts per year. When sown it is usually combined with timothy, which is also non-aggressive in the young plant stage. Such timothy meadow fescue leys, sometimes with the addition of cocksfoot, provide a possible alternative to the usual ryegrass-based leys. Meadow fescue can also be used as a non-aggressive companion grass for lucerne.

Cultivars. Early cultivars head at about the same time in May as Italian ryegrass, lates about a week or ten days later. The early rather stemmy Danish Commercial (now obsolete) was largely superseded by Aberystwyth S 215 and the later S 53. Of these, S 215 retains its importance in the 1970s as an early cultivar, but S 53 has been largely replaced by higher yielding late cultivars from the Netherlands. In 1978/9 a total of 19 cultivars were listed; all these were diploids, and autotetraploid meadow fescues do not appear to show promise.

Hybrids between meadow fescue and perennial ryegrass occur fairly commonly and have been named × *Festulolium loliaceum* (Huds.) Fourn.; these may be diploid or triploid but are always sterile. Fertile allotetraploids have however been developed at Aberystwyth, and potential cultivars of this type are under trial. If successful they may well prove very useful additions to the range of herbage grasses available for use in Britain.

Festuca arundinacea Schreb. (*F. elatior* var. *arundinacea* (Schreb.) Celak.). **Tall Fescue**

A very variable species, similar to meadow fescue, but always larger and coarser. It is only the finer forms (i.e. those nearest to meadow

fescue) which are of any agricultural importance, the larger forms being stiff, harsh-leaved plants of roadsides and sea-coast of little or no grazing value. It can be distinguished from meadow fescue by the larger panicles, with all branches bearing three or more spikelets, by the pointed or shortly-awned lemmas and by the ciliate auricles. Most forms are very early, with heavy spring yields. Seedling growth is slow, in spite of the large diaspore (about 500 000 per kg), and tall fescue is difficult to establish. Once established, it is persistent and drought-resistant. It is however of low palatability and may be of low digestibility; the latter feature appears in some cases to be due not only to the coarseness of the herbage, but to the presence of a compound perloline, which by inhibiting the normal gut flora of the ruminant animal reduces the digestion of cellulose. Thus although tall fescue can outyield perennial ryegrass in total dry matter under any but the best conditions, its disadvantages severely restrict its use except for special purpose grass drying under dry conditions, and tall fescue seed accounts for only some 0·5% of the total grass seed use in Britain.

Cultivars. Eight cultivars only were listed in 1978/9, including Aberystwyth S 170 and Conway and one amenity variety. Earlier trials of North African forms showed them to be insufficiently winter hardy, but potential cultivars derived from material from the south of France appear more promising. Tall fescue is a hexaploid, but crosses with perennial ryegrass are possible, and might be of value; it has indeed been suggested that some tall fescues may already incorporate genetic material derived from perennial ryegrass. Crosses of tall fescue with Italian ryegrass could be of value for conservation.

Festuca rubra L. **Red Fescue**

Small, needle-leaved grasses, agriculturally important only on hill-grazings, but useful for lawns and sports turf. Very variable.

Inflorescence. A rather narrow, open panicle, up to 60 cm high. Spikelets small, about 10 mm, four- to eight-flowered.

'*Seed*'. Caryopsis enclosed in palea and round-backed lemma, tapering into fine terminal awn; hairy in some forms; about 1·5 million per kg.

Vegetative characters. Perennial, with both intra- and extra-vaginal

shoots, usually creeping (except Chewing's fescue) by slender, brownish rhizomes. Leaves permanently folded, bristle-like (except on flowering shoots), auricles and ligule small, sheaths closed, often reddish (illustration p. 199).

Agricultural importance. Red fescue varies considerably, but in its better forms it is, in spite of its needle-leaves, a palatable grass of fair nutritive value. Under very good conditions of irrigation and high nitrogen a total dry matter yield comparable to that of perennial ryegrass has been recorded, but the digestibility falls rapidly, and the yield at 65 D-value can be less than one quarter of that of the ryegrass. The growing season is rather short, but production is relatively level from May to August, and declines much less steeply with reduced fertility than that of ryegrass. Red fescue is thus a valuable species for poor conditions, and although undesirable in good lowland grassland is one of the most useful grasses for hill and mountain grazings. Specialized ecotypes are a valuable constituent of saltmarsh grazings. Red fescue is rarely considered worth sowing as a herbage grass; the percentage establishment is low, and the seed, partly owing to the demand for it for sports turf, somewhat expensive, particularly for use on the poor land to which alone it is suited.

Forms

F. rubra L. subsp. *rubra* **Creeping Red Fescue**

This is the typical form of red fescue with well developed rhizomes, the commoner form in Britain, and very variable in natural habitats. Numerous mainly continental cultivars are available, the majority intended for amenity use. Aberystwyth S 59, which has rather softer lighter-green leaves and is more winter green than many of the wild forms, was originally bred as a grass for hill-reclamation, but has been mainly used for amenity purposes.

F. rubra L. subsp. *commutata* Gaud. (*F. rubra* var. *fallax* (Thuill.) Hack.). **Chewing's Fescue**

A non-creeping form of red fescue occurring in hill pasture, but usually less common than the creeping form. Introduced into New Zealand, where it was used as a constituent of seed mixtures for hill pastures, and seed later exported to Britain with the name of the original New Zealand seed producer, Chewing. Extensively used here for sports turf, Chewing's fescue is the main ingredient in most

Fig. 53. Small fescues. 1, panicle, ×½. 2, spikelet, ×3. 3, 'seed', ×10 of A, red fescue; B, sheep's fescue. C, viviparous fescue (no 'seed' produced).

fine lawn seeds mixtures, but is not persistent under hard wear. Available in numerous cultivars.

Festuca ovina L. **Sheep's Fescue**

A bristle-leaved perennial very similar to red fescue, but always tufted, with all tillers intravaginal, and with split leaf-sheaths. Panicle and 'seed' not readily distinguished from red fescue, although usually somewhat smaller and with shorter awns. Occurs in similar or rather poorer situations, and may be the main species of hill pasture. Generally less valuable as grazing than red fescue; estimated to have a useful productivity about a quarter of that of perennial ryegrass. Not sown for agricultural purposes, and rarely used for lawns, but a few cultivars are listed.

Related forms are *F. tenuifolia* Sibth. (*F. ovina* subsp. *tenuifolia* (Sibth.) Peterm.), fine-leaved fescue, with shorter narrower leaves and smaller awnless 'seeds', sometimes recommended for lawns and available in several cultivars; *F. longifolia* Thuill., hard fescue, a rather larger introduced species of continental origin, also available in a number of cultivars; and *F. vivipara* (L.) Sm. (*F. ovina* var. *vivipara* L.), viviparous fescue, resembling fine-leaved fescue, but always viviparous, i.e. spikelets becoming leafy and developing as young plants which may root if they come in contact with the ground. No seed is therefore formed. Common in wet mountain pasture and retaining the viviparous habit if transplanted to lowland.

VULPIA

A genus of small annual grasses, sometimes included in *Festuca*, with similar panicles, but very slender long-awned 'seeds'; flower with one stamen only.

Vulpia bromoides (L.) S. F. Gray, **rat's-tail fescue** (squirrel-tail fescue, 'hair'), is an annual with panicle up to 50 cm high, occurring in poor, under-grazed dry grassland, and sometimes as a weed of grass seed crops, especially perennial ryegrass. The panicle is able to develop during the period the field is laid up for seed, and some rat's-tail is shed before harvest, so that if a seed crop is taken several years in succession, an infestation of this weed may build up. Although the seed is much more slender than ryegrass, it is a difficult impurity to clean out, and may cause some clogging of screens. Under normal grazing conditions rat's-tail is not a serious weed, soon dying out if not allowed to seed.

Vulpia myuros (L.) C. C. Gmel., is a name which is often used to include this species; it refers strictly to a closely-related but much less common grass of waste places, distinguished by the panicle not being completely exserted from the upper leaf-sheath.

CYNOSURUS. DOG'S-TAILS

Panicles with very short branches, spike-like in appearance. Fertile spikelets similar to those of *Festuca*, but sterile reduced spikelets also present.

Cynosurus cristatus L. **Crested Dog's-tail**

A common perennial of rather poor pastures, occasionally sown but not of great agricultural value.

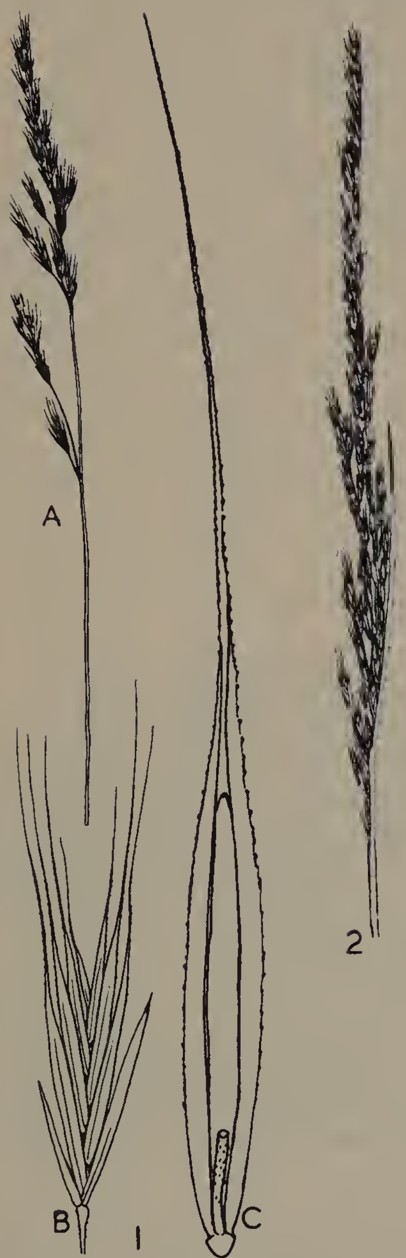


Fig. 54. 1, Rat's-tail fescue, *Vulpia bromoides*: A, panicle, $\times\frac{1}{2}$. B, single spikelet, $\times 3$. C, 'seed', $\times 10$. 2, panicle of the closely-related *V. myuros*, $\times\frac{1}{2}$.

Inflorescence. A one-sided spike-like panicle some 50 cm high. The very short panicle branches bear both fertile and sterile spikelets, the latter towards the outside, so that the fertile ones are largely hidden. Fertile spikelets some 5 mm long, with two nearly equal pointed glumes and from three to five florets. Sterile spikelets of about the same size, but with glumes and lemmas represented only by narrow, bristle-like structures.

'*Seed*'. Caryopsis enclosed in lemma and palea, *c*. 4 mm long, 1·5

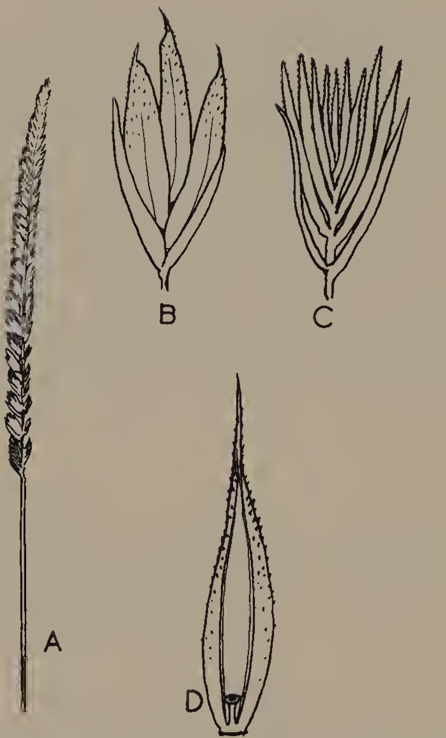


Fig. 55. Crested dogstail. A, panicle, $\times\frac{1}{2}$. B, fertile spikelet, $\times 6$. C, sterile spikelet, $\times 6$. D, 'seed', $\times 10$.

million per kg. Lemma narrow, rounded on back, sharply-pointed or very shortly-awned, rough on upper part. The yellowish-brown colour is very characteristic; 'seeds' all bright yellow may be an indication of under-ripeness, but there are nearly always sufficient yellow 'seeds' in a sample to make recognition easy.

Vegetative characters. A tufted, rather small, glabrous perennial, with leaves folded in bud, shoots oval in section. Leaf-blades short, stiff, tapering, deeply-ribbed above, shiny below; ligule very short, blunt; no auricles. Sheaths split, yellow at base (illustration p. 199).

Agricultural importance. A fairly palatable grass, but its small size and short leaves result in a low yield. It is hardy, winter-green and persistent under low-fertility conditions, and therefore often found in quantity in rather poor upland pastures. It may be sometimes worth sowing under such conditions, but requires careful management, as the inflorescence is very wiry and unless kept grazed down early, quickly becomes unpalatable, and is therefore able to produce and shed seed even under grazing conditions. Such self-seeding may result in the dog's-tail becoming dominant, with a resultant low pasture yield.

Dog's-tail is sometimes recommended for lawns and playing-fields, but although its stiff, short foliage is very suitable, the wiry inflor-

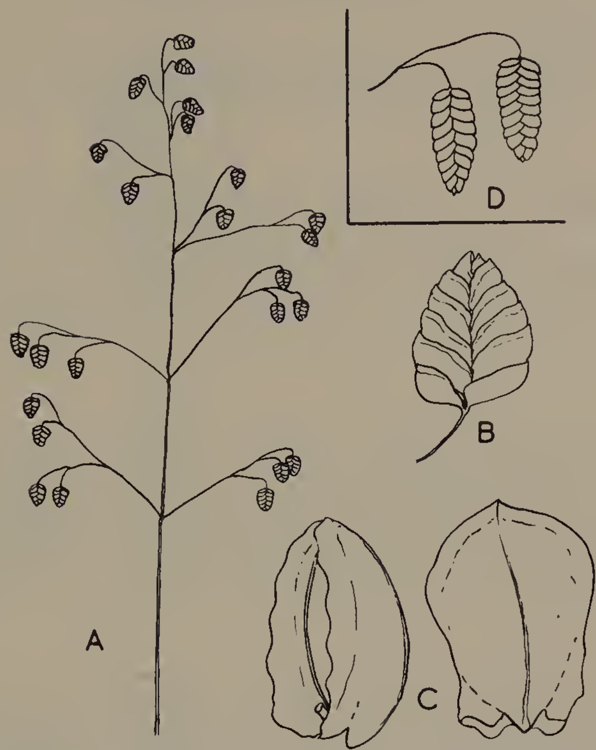


Fig. 56. Quaking grass, *Briza media.* A, panicle, ×½. B, spikelet, ×3. C, 'seed', side and dorsal views, ×10. D, two spikelets of *Briza maxima,* ×½.

escence stalks often prove impossible to mow cleanly; some amenity cultivars are available.

Cynosurus echinatus L., rough dog's-tail, is an introduced annual of no agricultural value, distinguished by its irregular, much broader panicles and long-awned lemmas.

BRIZA. QUAKING GRASSES

Briza has a spreading panicle, with pendulous, very broad spikelets; glumes and lemmas rounded, almost as broad as long.

Briza media L., **common quaking grass,** is a low-yielding perennial of poor grassland, fairly common, but rarely present in great quantity, and of little agricultural importance. Panicles are spreading, up to 50 cm high, branches flexuous, very slender so that the pendulous spikelets 'quake' in the wind. Spikelets, small, roughly triangular in shape, some 5 mm long with *c.* eight florets. Glumes and lemmas very broad, blunt, awnless, cordate at base.

B. minor L., lesser quaking grass, is an annual with similar but smaller spikelets found occasionally in S. England; *B. maxima* L. is a Mediterranean annual with very large, ovate spikelets, sometimes cultivated in gardens for its ornamental panicles.

DACTYLIS. COCKSFOOT

Panicle spreading but ultimate branches short, lemmas sharply keeled.

Dactylis glomerata L. **Cocksfoot,** Orchard Grass (U.S.A.)

A high-yielding perennial of major importance, frequently sown in leys. Tetraploid; a number of related diploid species occur in southern Europe.

Inflorescence. Panicle large, up to 1 m, primary branches long, so that the general outline is that of a spreading panicle, but ultimate branches short, so that the spikelets are crowded together in dense clumps (glomerata=clumped). Spikelets flat, 6–9 mm long, three- to five-flowered, glumes and lemmas strongly keeled.

'Seed'. Caryopsis enclosed by lemma and palea, 5 mm, 1 million per kg. Lemma very sharply keeled, so that 'seed' is compressed laterally and tends to lie on its side. Lemma very shortly-awned, rough, pale brown, hairy on keel, curved or twisted. The upper florets of the spikelet do not separate readily on threshing, and double or treble 'seeds' are frequent in some samples.

Vegetative characters. A stout, tufted, glabrous perennial, tillers all intravaginal, large. Leaves folded in bud, tillers very flat. Leaf-blades broad, long, tapering, dull grey- or blue-green on both surfaces, upper flat with single median line of motor-tissue, lower deeply-keeled. Auricles absent, ligules large, white, conspicuous. Leaf-sheaths broad, thick, fleshy, white at base, strongly-keeled, rather persistent, dying off pale brown (illustration p. 200).

Agricultural importance. Cocksfoot is a valuable high-yielding perennial, but somewhat coarser and less palatable than perennial ryegrass, and with digestibility falling much more rapidly, so that its primary yield at 66 D-value is under half that of ryegrass. It will however tolerate somewhat lower fertility than ryegrass, gives better late autumn grazing, and is much more drought-resistant. This latter feature is its particular merit, and it is essentially a grass for low rainfall areas and for free-draining soils. It is sometimes sown alone under such conditions, and is commonly included in general-purpose leys where some degree of drought resistance is required. Establishment from seed is fairly good (40%), but the seedling growth is rather

Fig. 57. Cocksfoot. A, panicle, $\times\frac{1}{2}$. B, part of panicle to show clustered spikelets, $\times 3$. C, single spikelet, $\times 3$. D, 'seed', side and ventral views, $\times 10$.

slow, and cocksfoot does not compete well with the ryegrasses in the first year. Aggressiveness in later years is very dependent on management. The thick fleshy leaf-sheath bases act as a food reserve, and cocksfoot is very markedly favoured by long rest periods, which enable such reserves to be built up. Under lenient grazing it may become dominant in an originally mixed sward, individual plants building up into large and often rather unpalatable clumps.

Cultivars. The commercial cocksfoot used during the early part of this century was of American or Danish origin, stemmy and erect and prone to form unpalatable coarse clumps if not well managed. Three

Aberystwyth-bred varieties became available in the 1930s; of these S 143, late-flowering, persistent and semi-prostrate, was the easiest to manage to avoid clump formation, and rapidly became the most commonly grown cocksfoot. It is however relatively low-yielding, and has been largely replaced by the two other Aberystwyth cultivars, S 37 which is medium early-flowering, and S 26 late-flowering; both are higher yielding than S 143 and sufficiently persistent for most purposes. True earlies heading before mid-May are not generally used, since a first conservation cut would have to be in early May to give a 65 D-value. Other cultivars available are Tenderbite from the Netherlands, with softer leaves, and Prairial, of French origin, with persistence equal to that of S 143 and higher yield. Saborto, bred at Aberystwyth, is a cross between S 37 and an autotetraploid derived from a Portuguese diploid form; it has the very early spring growth of its southern parent, and outyields S 37 over the whole year, but is doubtfully winter-hardy. A total of 18 cocksfoot cultivars were included in the 1978 United Kingdom national list.

POA. THE MEADOW-GRASSES

Panicle spreading, spikelets small, flattened. Lemmas keeled, awnless. Leaves folded, with two lines of motor tissue.

Poa trivialis L. **Rough-stalked Meadow-grass**

A common and fairly useful grass of damp soils, rarely sown.

Inflorescence. Panicle spreading, open and feathery in appearance, with numerous small spikelets, 3-4 mm long, usually three- to four-flowered. Culm immediately below lowest node of panicle sometimes slightly rough with minute, downward-pointing spines (it is to this that the not very helpful common name refers).

'*Seed*'. Caryopsis, with lemma and palea, with at the base a *web* of fine, cottony hairs (removed during cleaning). 'Seed' small, *c*. 3 mm, 4 million per kg, triangular in cross-section owing to sharply-keeled lemma; tapering narrow-oval in side view. Lemma five-nerved, awnless, hairy on lower half of keel only.

Vegetative characters. A stoloniferous creeping perennial (loosely-tufted under dry conditions). Leaves folded in bud, tillers flat. Leaf blades bright green, soft, tapering, rather short, shiny below, rather dull above, but not ribbed, with a double line of motor

tissue. Auricles absent, ligule pointed, short on barren tillers but long on upper leaves of flowering tillers. Sheaths split, flattened, pale (illustration p. 200).

Agricultural importance. Rough-stalked meadow-grass is a palatable but rather low-yielding grass very common in most damp lowland grassland. Under good conditions with ample moisture its yield is perhaps three-quarters of that of perennial ryegrass, with a similar level of digestibility. Productivity in the later part of the year is low. It will tolerate somewhat lower fertility than ryegrass, but it is not a grass of poor conditions, and is very intolerant of drought, and is not usually long-lived. The seed is light-sensitive (requires light for good germination) and establishment from drilled seed may be as low as 5%. It is thus not often sown now. Under moist conditions surface seed germinates readily, and rough-stalked meadow-grass thus tends to volunteer in leys and lowland pastures. In small quantities, say 10% or less, it may add slightly to the productivity of a ley, but in larger quantity, where it is occupying space which could be filled by more productive species, it could properly be regarded as a weed. Under such conditions it can be controlled by herbicides such as methabenzthiazuron, or by low concentrations of paraquat, or rather less effectively of dalapon, to which most cultivars of perennial ryegrass are resistant. In old pasture, where the expected level of production is lower, rough-stalked meadow-grass would generally be regarded as an acceptable constituent of the herbage. It is frequently present in lawns and sports turf, but is not normally intentionally sown.

Rough-stalked meadow-grass may under some conditions appear as an arable weed; it is then a loosely-tufted plant with leaves broader and rougher than under grassland conditions. Infested areas such as grass seed crop stubbles may need to be left unploughed until surface seed has germinated, so that the seedlings can be killed with paraquat.

Cultivars. A number of continental cultivars are included in the United Kingdom national list and are sometimes offered by British seeds firms, but are rarely used here.

Poa pratensis L. **Smooth-stalked Meadow-grass**

A common grass of rather low value, never normally sown.

Inflorescence. A spreading panicle, more compact and with spikelets larger than rough-stalked, 5–6 mm long with from four to five florets.

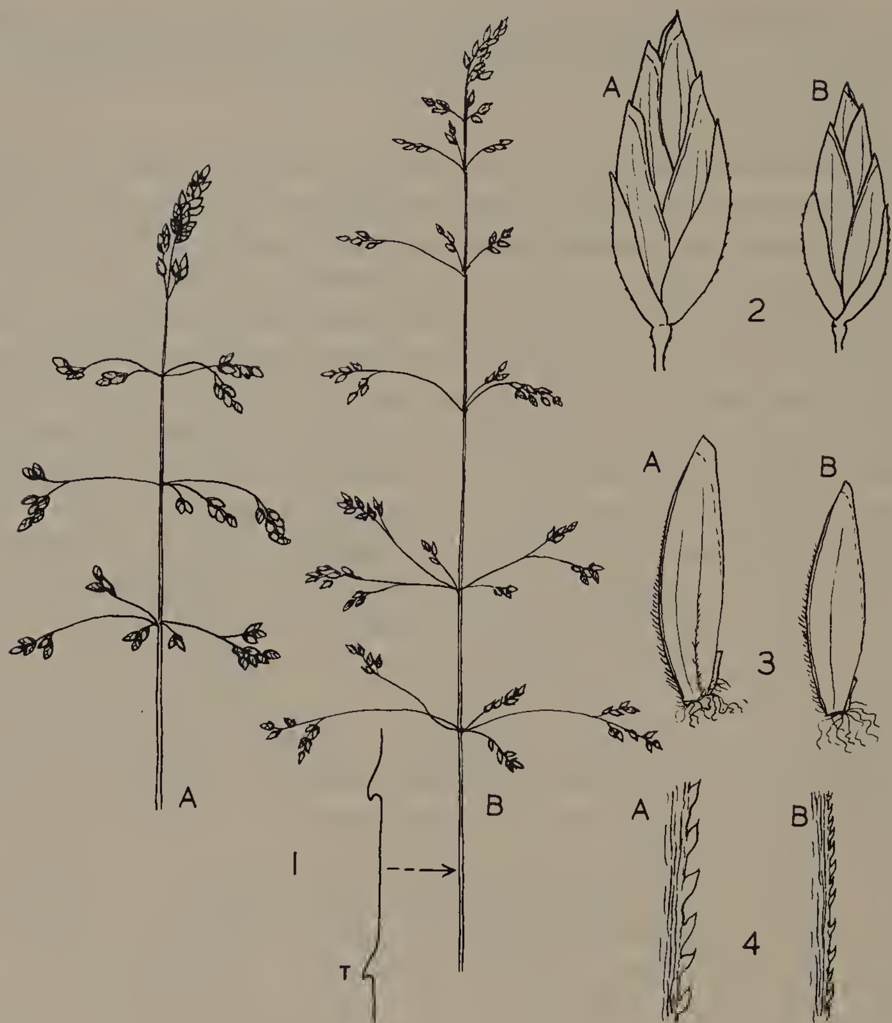


Fig. 58. Meadow-grasses. 1, panicle, ×½. 2, spikelet, ×7. 3, 'seed' (unmachined, web and hairs still present), ×10. 4, teeth on nerves of palea, ×60, of A, smooth-stalked, and B, rough-stalked meadow-grass. T, margin of culm of rough-stalk, ×60, to show teeth sometimes present.

'Seed'. Very similar to rough-stalked, but rather broader, with blunter lemma, about 3 million per kg. It can be distinguished in the fresh state by the presence of hairs on the intermediate nerves of the lemma as well as on keel (keel only in rough-stalked), but these are usually removed together with the web during the seed-cleaning. The slightly coarser teeth on the keels of the palea of smooth-stalked may also be used as a distinction, but it is necessary to dissect out the palea to observe these.

Vegetative characters. A rhizomatous creeping perennial, with rather stout, white, underground stems bearing scale and transitional leaves. Foliage leaves similar to those of rough-stalked, but blade

longer, stiffer, darker green, parallel-sided narrowing abruptly to a boat-like tip, ligule always blunt, sheaths smooth (illustration p. 200).

Agricultural importance. The stiff leaves of smooth-stalked are rather unpalatable and of low digestibility, and it has little to recommend it, other than its drought-resistance and ability to withstand treading. It is a very common grass, being found in small amount in most old pastures, but is rarely a dominant species. Establishment from seed is usually poor, and in Britain it is even less commonly sown than rough-stalked although under the rather more difficult conditions of the eastern U.S.A. it is highly valued as a pasture grass, under the name of Kentucky bluegrass.

Cultivars. Poa pratensis, as usually defined, is a variable species, and includes plants with chromosome number varying from 28 (tetraploid) to 124. Many of the higher polyploid forms are apomictic, i.e. produce seed without fertilization, and therefore do not show segregation. Apomictic cultivars may thus consist of a single genotype only, and some are exceptional amongst grass cultivars in that they can be distinguished in the seed (diaspore) stage on morphological characters. Numerous cultivars have been developed in Europe and America, and 22 were included in the 1977 British list. They are, however, little used, since even for sports turf, where its hard-wearing characters might make it of value, smooth-stalked meadow-grass is rarely sown in Britain, as the rate of establishment of a usable sward from seed is regarded as too slow.

Poa annua L. **Annual Meadow-grass**

An annual or ephemeral, daylength-indifferent and producing small panicles 5 to 25 cm tall at almost all times of year. Spikelets few, relatively large; 'seed' shorter, broader and blunter than in rough-stalked meadow-grass, webless, but hairy on all nerves of lemma. Vegetatively it somewhat resembles rough-stalked, but has shorter, blunter leaves, broader in proportion and often transversely crinkled. Ligule with rounded point, more conspicuous than on vegetative tillers of rough-stalked (illustration p. 201).

A very common grass, rapidly establishing from seed on any bare ground. Frequent in grassland, where its presence in any quantity is usually an indication of earlier bare patches. Palatable, but yield very low, and drying up completely in hot dry weather. A common but usually unimportant arable weed; may invade grass seed crops, and 'seed' not infrequent as a weed impurity. Controllable by

cultivations, terbutryne, or methabenzthiazuron. A very common unsown but sometimes useful constituent of lawns and sports turf, persisting and self-seeding under close mowing.

Tetraploid; probably an amphidiploid between two similar but much less widespread diploid species *Poa infirma* H.B.K. and *P. supina* Schrad.

Poa compressa L., **flat-stemmed meadow-grass,** a rhizomatous perennial with rather rough, greyish leaves and small panicles with distinctly flattened stem occurs in dry lowland grassland, but rarely in quantity. Cultivated in North America as Canadian bluegrass. ***Poa nemoralis*** L., **wood meadow-grass,** a tufted perennial, with slender, dark-green leaves and large spreading panicles, and with nodes of flowering tillers black, is found in woods and is sometimes recommended for lawns in shade; a single cultivar was listed in 1977.

In view of the difficulty of separating 'seeds' of different species of *Poa*, the 1976 regulations for fodder plant seeds allow greater tolerances than usual where seed of one species is contaminated by seeds of another *Poa* species.

Puccinellia maritima (Huds.) Parl., **sea meadow-grass** (distinguished from *Poa* by rounded, not keeled, lemmas) and related species provide useful salt-marsh grazing.

BRACHYPODIEAE

BROMUS. THE BROME GRASSES

Inflorescence festucoid, with lemmas either keeled or rounded on back and with dorsal awn. Ovary with hairy process above lateral styles, and starch grains simple, not compound, and therefore referred to separate tribe. A large genus, divisible into a number of sections, sometimes treated as separate genera. British species mainly hairy, unpalatable weeds.

Bromus mollis L. Soft Brome

Usually annual, common in over-hayed grassland, and occasionally an impurity of grass seed.

Inflorescence. Spreading panicle with large, oval spikelets, 15–20 mm long, eight- to ten-flowered, with lemmas of adjoining florets overlapping, lemmas hairy, awned.

'*Seed*'. Lemma shortly hairy, very much broader than caryopsis and palea and tending to stand out at sides, variable, *c*. 10 mm long, with fine, rough dorsal awn of about the same length. Rachilla barrel-shaped, upper separation surface sloping. Typical large 'seeds' are considerably bigger than those of ryegrass, but the smaller 'seeds' and those in which the lemma is more closely rolled about the palea, are difficult to remove from ryegrass and similar sized seed.

Vegetative characters. Tufted annual or sometimes biennial, autumn germinating, leaves rolled, shoots round. Leaf-blades broad, conspicuously twisted, dull grey-green, hairy, soft, no auricles, ligule blunt. Sheaths closed, hairy, keeled, pale (illustration p. 204).

Agricultural importance. An unpalatable grass spreading rapidly by self-sown seed if not prevented by hard grazing or early cutting; it is therefore most common in grass fields cut for hay each year, particularly where hay is cut late enough for the bulk of the brome seed to have ripened. Control by hard grazing; soft brome is not completely unpalatable and will usually be eaten down in spring and again in autumn; not persistent if not allowed to seed. It is, of course, favoured by seed-production conditions, and was formerly a common weed in seed crops of perennial ryegrass, particularly where these were harvested several years running.

Numerous closely related species exist, including *B. arvensis* L., field brome, with rather lighter green leaves and narrower spikelets, an uncommon grassland weed in Britain, but formerly sown for hay in northern Europe, and *B. secalinus* L., rye brome, with very broad spikelets with florets spreading at maturity, and almost glabrous leaf-sheaths, at one time common as a weed of cereals.

Bromus sterilis L. (*Anisantha sterilis* (L.) Nev.), **barren brome,** is a very common annual with large, drooping panicles of very large wedge-shaped spikelets, up to 5 cm long, consisting of from six to ten florets. The 'seed' is up to 20 mm long, with an even longer dorsal awn. Although often abundant in field hedges and occasionally spreading by seed into cultivated land, it is rarely a serious weed, as it does not persist in a grazed sward, and the 'seed' is not difficult to remove from seed corn, but is perhaps increasing in winter cereals.

Bromus erectus Huds. (*Zerna erecta* (Huds.) Panz.), **upright brome,** is a tufted, slightly hairy perennial with erect panicles and parallel-sided spikelets. It is coarse and unpalatable and may become dominant in under-grazed grassland on limestone soils.

Bromus ramosus Huds. (*Zerna ramosa* (Huds.) Lindm., *Bromus asper* Murr.), **wood brome,** is a common hairy perennial distinguished

Fig. 59. Brome grasses. 1, Soft brome, *Bromus mollis:* A, panicle, $\times\frac{1}{2}$; B, spikelet, $\times 3$; C, 'seed', $\times 10$. 2, spikelet of *B. arvensis,* $\times 3$. 3, spikelet of *B. secalinus,* $\times 3$.

by its very large, drooping panicle, almost confined to woodland, and rarely appearing on farmland. *Bromus inermis* Leyss. (*Zerna inermis* (Leyss.) Lindm.), awnless brome, is an almost hairless, strongly rhizomatous perennial, with cylindrical spikelets, awns very short or absent. Not native, and although extensively grown (as 'brome', or 'smooth brome') in N. America, is not generally considered worth cultivation in Britain. *Bromus willdenowii* Kunth. (*B. unioloides* Willd., *Ceratochloa unioloides* (Willd.) Beauv.), Schräder's brome or rescue grass, is another species cultivated in America and in Europe, but only occasionally introduced in Britain. It is a large-growing perennial with broad leaves and very large flat spikelets. The rather similar but less hairy octoploid *B. carinatus* Hook. & Arn., sweet

brome, cultivar Deborah, has given promising results in trials as a possible cocksfoot replacement.

BRACHYPODIUM. FALSE BROMES

Perennials of no agricultural value, resembling the bromes, but with spikelets in a simple raceme, not panicle, and awns terminal, not dorsal.

Brachypodium pinnatum (L.) Beauv., **tor grass** or heath false-brome, is a stout, coarse, rhizomatous perennial of chalk and limestone soils, with harsh, yellowish-green, slightly hairy leaves. Inflorescence a simple raceme of short-stalked, erect, cylindrical, often curved, many-flowered spikelets. Lemmas glabrous, rounded on back, shortly-awned. Tor grass rapidly becomes unpalatable and may spread to become dominant in undergrazed chalk downlands and similar areas.

Brachypodium sylvaticum (Huds.) Beauv., **wood false-brome,** differs in having no rhizomes, thinner, papery, more hairy leaves and less smoothly-cylindrical, straight spikelets, with more tapering, longer-awned, hairy lemmas. It is confined to shady conditions, and although often abundant in hedges, is not found in agricultural grassland except occasionally as a relic of cleared woodland.

Fig. 60. Wood false-brome. Raceme, $\times\frac{1}{2}$. Spikelets on short stalks.

HORDEAE

AGROPYRON. COUCH GRASSES

Inflorescence a spike, with a single, many-flowered spikelet at each node. Each spikelet has much the same structure as that of the *Festuceae,* with a pair of rather short glumes, and four or more florets. In Britain, one species only is important, and that as an arable weed; some foreign species are cultivated as forage grasses.

Agropyron repens (L.) Beauv. **Couch,** Twitch

A common and serious perennial weed of arable land.

Inflorescence. A rather stiff spike with a single three- to eight-flowered spikelet some 15 mm long at each node. Two glumes present per spikelet; spikelets flat side on to rachis (not edgewise, with one glume only, as in ryegrasses). Lemma variable; blunt, pointed or with terminal awn up to half its own length.

'Seed'. Lemma rough, keeled towards the apex, 7 mm or more long; awned or awnless; rachilla cylindrical, rough, with terminal pit. Couch is not highly self-fertile, and since large areas may be occupied by a single clone, relatively few 'seeds' contain a caryopsis; in empty spikelets the florets often do not separate. Spread by 'seed' is relatively unimportant, and special regulations apply to couch as an impurity in fodder plant seeds at the Higher Voluntary Standard only.

Vegetative characters. Perennial, with very extensive, stout, white, sharply-pointed rhizomes, spreading to form loose tufts of tillers above ground. Leaves rolled in bud, shoots round. Leaf blades large, broadest in middle, dull green, variably hairy. Auricles present, usually small, ligule short. Sheaths open, not keeled, pale, variably hairy (illustration p. 203).

Agricultural importance. Couch rarely occurs in any quantity in grassland; its habit of growth makes it essentially a grass of disturbed soil and open vegetation, and it is as an arable weed that it is important. Spread by seed may take place, but it is mainly due to its very great capacity for vegetative spread that it is so common. Found on all types of soils, but perhaps more serious on the heavier ones, owing to the greater difficulty of carrying out the necessary cultivations, par-

Fig. 61. Couch, *Agropyron repens*; A, spike in face and side views, × ½; B, spikelet of awnless form, ×3; C, of awned form; D, 'seed', ×10. E, spikelet of bearded wheatgrass, *A. caninum,* ×3, for comparison with C.

ticularly under wet conditions. Control by cultivation involves the killing of the rhizomes by working them to the surface to dry out; even quite small pieces of rhizome, providing that they include at least one node, are capable of growth. Repeated rotary cultivation has also been used, but has tended to be replaced by repeated spraying of paraquat, the repeated defoliation leading to the exhaustion of the food reserves in the rhizomes. Other herbicides can also be used; T.C.A. acts on the rhizomes and must be worked into the soil; glyphosate, dalapon or aminotriazole can be used as foliar sprays; a few selective herbicides for use in dicotyledonous crops only are also available.

Agropyron pungens (Pers.) Roem. & Schult., with tough rachis, and *A. junceiforme* Löve, with very broad spike readily breaking at nodes, are sea-coast plants of similar habit to couch; *A. caninum* (L.) Beauv., tufted couch or bearded wheat-grass, is a tufted non-creeping perennial with slender spikes and long-awned lemmas, found in woods.

Triticum, the wheat genus, is closely related to *Agropyron,* and hybrids are possible between the two genera. It differs in its broader

glumes, larger caryopsis and in the fact that only the lower flowers on the spikelet are fertile. *Secale,* the rye genus, with two florets only per spikelet and very narrow glumes, is also closely related. No wild species of these two genera occur in Britain. For wheat and rye as cultivated cereals, see Chapter 5.

Elymus has spikelets somewhat similar to those of *Agropyron,* but two spikelets are borne side by side, at each node of the rachis, instead of only one. *E. arenarius* L., sea lyme grass, is a seacoast perennial, with broad, very hard, harsh grey-blue leaves, stout rhizomes and large spike, sometimes planted on sand-dunes to control wind erosion.

HORDEUM. BARLEYS

Spikes with three spikelets at each node; spikelets one-flowered only. *H. sativum* Pers., the cultivated barleys, with large caryopsis and tough rachis, is dealt with in Chapter 5; the smaller wild species are known as barley-grasses.

Hordeum secalinum Schreb. (*H. pratense* Huds.), **meadow barley-grass,** is a tufted, short-lived perennial of moist grassland, rather local in distribution. It is neither palatable nor high-yielding, and is to be regarded as a weed. It has hairy, rolled leaves and small auricles; the spike is small, with the centre spikelet at each node fertile, the lateral ones male only, and shortly-stalked. The two glumes of each of the three spikelets are very narrow, bristle like. The rachis is fragile—that is, the spike breaks up at maturity into single internodes to which the three spikelets remain attached. The 'seed' is thus a very complex structure consisting of a short length of rachis plus three complete, single-flowered spikelets, with the single caryopsis enclosed within the lemma of the central one. Its sharp-pointed and strongly-barbed character give it great powers of penetration, and it may cause irritation to grazing stock.

Hordeum murinum L., **wall barley-grass**, is a very common annual of disturbed waste ground, suburban roadsides, etc., very rarely becoming a farm weed. It is an annual, distinguished by its lighter-green leaves with larger auricles and its larger, broader spike, with the glumes of the central spikelet broad at the base, not bristle-like throughout. The spike breaks up in the same way as that of meadow barley-grass.

AVENEAE

Avena, the oat genus, as now defined, includes only the cultivated and

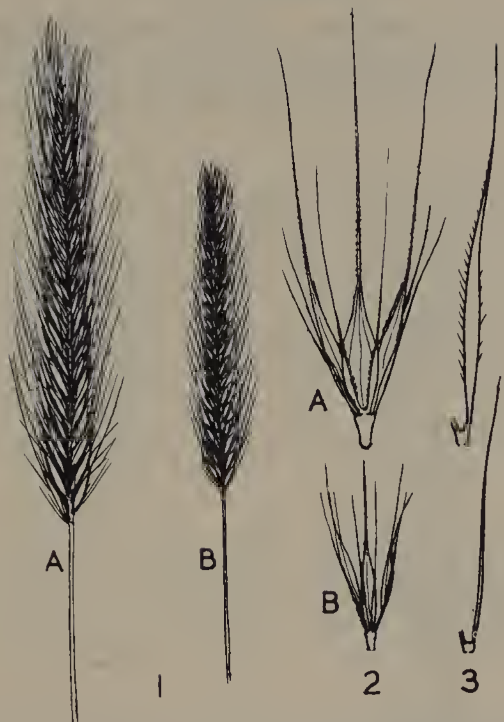


Fig. 62. Barley-grasses. 1, spike, ×½. 2, 'seed' (three spikelets attached to single internode of rachis), ×1. 3, glume of central fertile spikelet, ×3, of A, wall barley (*Hordeum murinum*), and B, meadow barley (*H. secalinum*)).

related wild oats, annuals with panicles of large, pendulous spikelets, with the florets surrounded by the many-nerved glumes. These are dealt with in Chapter 5. The following three genera (*Arrhenatherum, Trisetum* and *Helictotrichon*) of perennial oat-grasses were formerly included in *Avena,* but are clearly not very closely related to the cultivated oats, and are now kept separate.

ARRHENATHERUM

Spikelets erect, two-flowered, with few-nerved glumes. The generic name means 'male-awned'; the lower floret of the spikelet is male only, and is more conspicuously awned than the upper.

Arrhenatherum elatius (L.) J. & C. Presl.* **Tall Oat-grass**

A very common large grass, of little importance in present-day British agriculture. A tuberous variety is a serious arable weed of light soils.

* The name *Arrhenatherum avenaceum* Beauv., sometimes used, is not valid, since the species had already been named *Avena elatior* by Linnaeus, and the specific name (with the necessary change of gender) must be retained in the new genus.

Inflorescence. Erect panicles, 1 m or more high, usually rather dense. Spikelets 8–10 mm long, with two unequal translucent glumes and two florets. Lower floret male only, lemma blunt rounded, with

Fig. 63. Tall oat-grass. A, panicle, ×½. B, spikelet, ×3. C, 'seed' (whole spikelet without glumes), ×10.

very strong geniculate awn arising almost at its base. Upper floret smaller, hermaphrodite, and hence producing a caryopsis, lemma awnless or with short fine, straight dorsal awn.

'Seed'. This consists of the whole spikelet apart from the glumes—that is, the empty lemma and palea of the lower floret are present as well as those of the upper floret, which contains the caryopsis. The 'seed' is thus usually large, *c.* 10 mm long, about 330 000 per kg and bears two awns. It is difficult to clean and also to drill; in the U.S.A., where tall oat-grass is of greater importance than in Britain, some work has been carried out on the 'hulling' of the 'seed', so that the much smaller and more readily-drilled caryopsis only is sown.

Vegetative characters. Perennial, tufted; tillers large, leaves rolled in buds, shoots round. Leaf-blades long, broadest in middle, dull green, variably hairy. No auricles, ligule long. Sheaths split, hairy, pale. Roots chrome yellow (illustration p. 204).

Agricultural importance. Tall-oat is an early, high-yielding grass, but it is rather coarse and unpalatable, with somewhat bitter taste. It is very intolerant of hard grazing and treading. Although formerly included in some permanent pasture mixtures, it is unsuited to pasture conditions, and it is only in ungrazed turf, roadsides, etc., that it is common. If used agriculturally its proper place is in short leys for hay, on land too poor or too subject to drought and heat to support the better grasses; its high yield and rapid recovery from cutting are utilized in this way in France, and in parts of the U.S.A. too dry for timothy. Its use in Britain is now negligible; one cultivar listed 1977.

In the tuberous form, var. *bulbosum* (Willd.) Spenn., onion couch, the lower internodes of the shoots are swollen to form chains of bead-like corms 5–10 mm in diameter. These corms readily break apart, and each is capable of producing a new plant. This onion-couch form of tall-oat may therefore become a serious weed if it is present in arable land, owing to the practical impossibility of removing such round, bead-like structures by any form of mechanical cultivation. Chemical control measures as for *Agropyron repens* (p. 171) have some effect.

TRISETUM

All florets fertile; the lemmas are split at the top to form two slender, awn-like points which, together with the dorsal awn, give the 'three bristles' which is the meaning of the name.

Trisetum flavescens (L.) Beauv., **golden oat-grass,** also called yellow oat-grass, is a palatable but low-yielding perennial of dry, especially calcareous, pastures. It has a panicle similar to that of tall-oat, but much smaller, and with smaller three- to four-flowered spikelets, becoming distinctly yellow as it ripens. Vegetatively it is most easily recognized by its slightly hairy, rolled leaves, without auricles, with downward-pointing hairs on the split, pale sheaths. It provides useful sheep-keep on upland pastures, and may make an important contribution to the yield of downland swards, but is not considered worth including in seeds-mixtures, and 'seed' is rarely available in Britain.

An annual dry matter yield of some 4 000 kg/ha has been recorded for *Trisetum* grassland in Central Europe. (For illustration of vegetative stage see p. 204.)

Fig. 64. Golden oat-grass. A, panicle, $\times\frac{1}{2}$. B, spikelet, $\times 5$. C, 'seed', $\times$ 10.

HELICTOTRICHON

Larger spikelets, with all florets fertile, lemmas not two-pointed. *H. pratense* (L.) Pilger, meadow oat-grass, and *H. pubescens* (Huds.) Pilger, downy oat-grass, are two rather similar tufted perennials of minor importance, occurring in the same sort of semi-natural pasture as golden oat-grass, but less generally common. Downy oat-grass has more hairy leaves and is less strictly confined to dry conditions.

KOELERIA

Small spikelets on a compact, almost spike-like, panicle. The glumes are rather short and the lemmas awnless. *Koeleria cristata* (L.) Pers., crested hair-grass, is another perennial of dry, calcareous pastures, of very minor agricultural importance.

DESCHAMPSIA

Has spikelets with two florets only, both fertile; plants perennial.

Deschampsia caespitosa (L.) Beauv., **tussock grass** or tufted hair-grass, is a very large, unpalatable, tufted perennial forming dense clumps. The panicles are very large, silvery, spreading, with very numerous small spikelets. The spikelets have two flowers, each with a blunt lemma, short basal awn and hairy rachilla. Leaf blades broad, hard, dark green, deeply ribbed on upper surface.

Tussock grass is a serious weed of rather poor pastures on heavy or badly-drained soil; it establishes readily from seed and is extremely unpalatable, so that, unless prevented by hard grazing or cutting at an early stage, the seedlings quickly develop into large tufts and ultimately into the characteristic tussocks or 'hassocks'. If plants are allowed to reach this stage they are far too tough to be grazed off by any stock, and may even be impossible to mow closely; ploughing and reseeding is then the only method of improving the pasture, and even that may be impeded by the difficulty of ploughing large tussocks under. Susceptible to low concentrations of dalapon.

D. flexuosa (L.) Trin., **wavy hair-grass**, is a smaller grass with panicles only half the size of those of tussock grass. The panicle branches are flexuous (whence the common name); the comparatively few spikelets are slightly larger than those of the tussock-grass, and the awns longer and stouter. Vegetatively, wavy hair-grass is very different; it is a low-growing, loosely-tufted or slightly-creeping perennial with permanently-folded, bristle-like, short leaves. It, also,

Fig. 65. Hair-grasses. 1, panicle, ×½. 2, spikelet, ×3. 3, 'seed' in side and ventral views, ×10, of A, tufted hair-grass (tussock grass), and B, wavy hair-grass.

is very unpalatable and of no value for grazing, but is confined to acid hill and heath land, and does not invade sown pastures.

The genus *Aira,* in which the *Deschampsia* species were formerly included, is now regarded as covering only annual grasses with rather similar spikelets; of these, *Aira praecox* L. (*c.* 15 cm high, panicle compact, very early) and *A. caryophylla* L. (*c.* 30 cm, panicle spreading) are common but unimportant heath grasses.

HOLCUS

Spikelets of two florets, the upper male only, the lower hermaphrodite (the reverse of the position in *Arrhenatherum*).

Holcus lanatus L. **Yorkshire Fog**

A common and important perennial weed of grassland, and a common impurity of grass seeds.

Inflorescence. A spreading panicle, usually rather dense, but very variable in general appearance and in colour, which varies from green through almost white to pink. Spikelets *c.* 5 mm, with two florets almost completely hidden by the broad, keeled, hairy glumes. Florets small, lemmas half length of glumes, lower floret awnless, hermaphrodite and producing caryopsis, upper male only, with dorsal hooked awn, usually hardly extending beyond glumes.

'Seed'. Occurs in two states: (1) the whole spikelet including glumes giving a fairly large but proportionately very light 'seed' found as an impurity of ryegrass and similar seeds; (2) rubbed-out, as the caryopsis enclosed only in the short, ovate, shiny brown lemma and palea, with, or more commonly, without, the narrower, awned, empty lemma of the upper male floret; this stage is more commonly found as an impurity in samples of smaller grass seeds, such as timothy.

Vegetative characters. A loosely-tufted perennial, densely soft-hairy. Leaves rolled in bud, shoot round. Leaf-blades dull grey-green; auricles absent, ligule long; sheaths open, keeled, pale with conspicuous red veins (illustration p. 203).

Agricultural importance. Yorkshire fog has been reported as capable of giving, under good conditions, yields comparable to those of ryegrass, with good digestibility as measured by *in vitro* methods. It is however unpalatable, and is usually regarded as of very low value; its

useful productivity has been estimated as about one-third of that of perennial ryegrass. It is usually grazed only when very young, and thus often left to form conspicuous tufts, which, however, tend to die away in winter, and rarely reach very large size. Tolerant of acidity and of rather low fertility, and may spread rapidly if allowed to seed owing to under-grazing or to late hay-cuts; it is one of the commonest grass weeds of poorly-managed long leys, and is present in small quantity in all but the very best of old pastures. Susceptible to low concentrations of paraquat or dalapon, and also to asulam as used for dock or bracken control.

Although Yorkshire fog is to be regarded as a weed under lowland conditions, it has been used in temporary pioneer mixtures for mountain reclamation under extreme conditions, as giving rapid establishment to provide a sward somewhat better than the original vegetation, at low cost.

Holcus mollis L., **creeping soft-grass,** is primarily a woodland plant, but may occasionally become an arable weed. It is distinguished in the flowering stage by its larger, more acute glumes and by the long, nearly straight awn on the lemma of the upper male flower standing

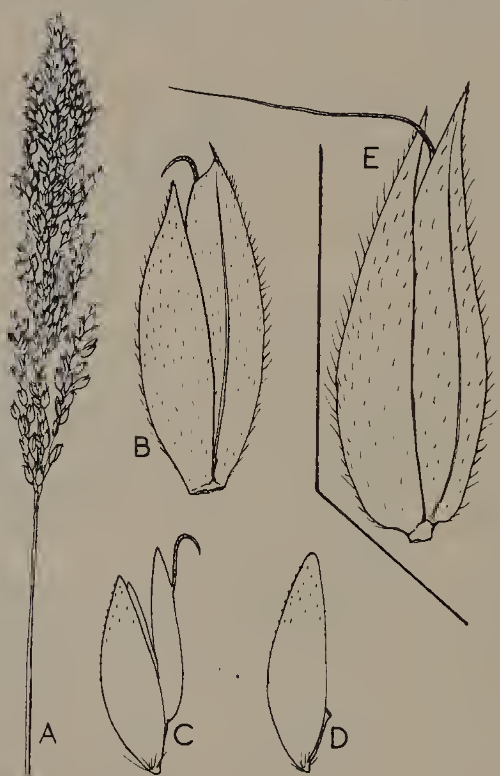


Fig. 66. Yorkshire fog. A, panicle, $\times\frac{1}{2}$. B, spikelet, $\times 10$. C, spikelet without glumes, $\times 10$. D, fertile floret only, $\times 10$ ('seed' may be B, C, or D). E, spikelet of creeping soft-grass, $\times 10$.

conspicuously out beyond them. Vegetatively it is distinguished by its creeping habit, with stout rhizomes and long, sprawling surface stems; the leaf-sheaths are less conspicuously red-veined, and less hairy than Yorkshire fog, but with a conspicuous ring of long hairs at the nodes. A common plant in rather dry woodland and in hedges, rare and usually unimportant in grassland, but may become a difficult arable weed of light land, behaving in the same way as couch. 'Seed' is not usually found as an impurity.

ANTHOXANTHUM

Spikelets which can be regarded as basically three-flowered, but only the uppermost is fertile, the two lower being represented only by their lemmas.

Anthoxanthum odoratum L. **Sweet Vernal Grass**

A common but unpalatable, low-yielding grass, frequent in rather poor pastures.

Inflorescence. A rather lax spike-like panicle; spikelets *c.* 8 mm long with unequal, pointed, thin, translucent, yellowish glumes, enclosing a pair of short, blunt, empty lemmas (representing the reduced, sterile lower florets) which are densely covered with dark brown hairs, and bear dark brown awns, that on the upper one geniculate and basal, and the other straight and dorsal. Between these two extra lemmas, and hidden by them, is the fertile floret, with short, shiny, awnless lemma and small palea. The palea is unusual in shape and may really represent the lemma of a fourth floret. Two stamens only are present, and no lodicules; the flower is protogynous and the stigmas emerge at the apex of the spikelet.

'Seed'. The whole spikelet above the glumes is set free as the 'seed', which thus consists of the caryopsis enclosed not only by its lemma and palea, but also by the two awned, hairy, extra lemmas. It is thus very distinct and easily recognized, but is not now normally in commerce in Britain, and rarely occurs as an impurity.

Vegetative characters. A loosely-tufted perennial, with rather dark-green, somewhat hairy foliage. Leaves rolled in bud, shoot round. Leaf-blades soft; auricles absent, ligule long; sheaths split, pale, hairy, with a conspicuous tuft of rather long white hairs at juncture of sheath and blade (illustration p. 203).

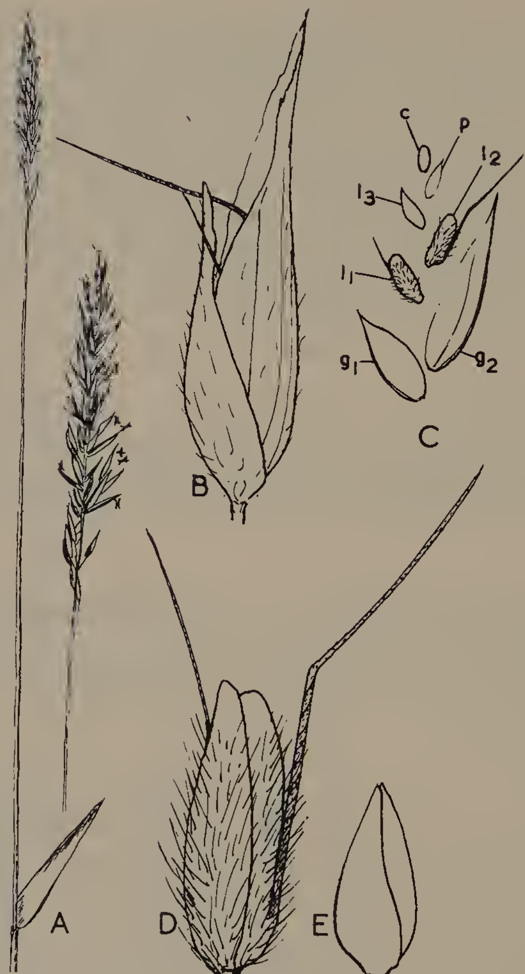


Fig. 67. Sweet vernal grass. A, panicles, $\times\frac{1}{2}$. B, spikelet, $\times 7$. C, diagram of spikelet dissected to show component parts. D, 'seed' (whole spikelet without glumes), $\times 10$. E, fertile floret only, removed from between extra sterile lemmas, $\times$ 10. g_1, g_2, glumes. l_1, l_2, extra lemmas representing sterile florets. l_3, p, lemma and palea of fertile floret. *c*, caryopsis.

Agricultural importance. Sweet vernal is a very common perennial occurring under a wide range of conditions, and tolerating drought and low fertility. It derives its common name from its early flowering and its sweet scent when dry; this scent is, however, due to the presence of coumarin which is bitter in taste and makes the grass unpalatable. This, combined with its low yield, has resulted in sweet vernal losing its former reputation as a useful grass; it is never now sown in Britain, and is regarded as a weed. Control is possible using low concentrations of dalapon.

PHALARIS

Resembles *Anthoxanthum* in structure of spikelet, but the two empty lemmas, representing the basal sterile florets, are reduced to small

Fig. 68. *Phalaris* species. 1, panicle, ×½. 2, spikelet, ×3. 3, 'seed' (caryopsis enclosed in lemma and palea, plus two narrow sterile lemmas), ×10, of A, canary grass, *P. canariensis*; B, reed canary grass, *P. arundinacea* (panicle shown in closed and open states); C, *P. tuberosa*.

scales, and the usual three stamens and two lodicules are present in the fertile floret. The two genera are usually placed in a distinct tribe, the *Phalarideae,* but *Anthoxanthum* shows close resemblances to the typical members of the *Aveneae*.

Phalaris canariensis L., **canary grass**, is a Mediterranean annual very occasionally grown in England as an arable, cereal-like crop for bird-seed. It has broad, oval, spike-like panicles up to 5 cm long, with large, very deeply-keeled green and white-striped glumes, completely enclosing the three florets of each spikelet. The threshed 'seed', as used for bird-seed, consists of the caryopsis enclosed in the hardened lemma and palea, pointed oval, *c.* 5 mm long, shiny but shortly-hairy, with the small, glabrous, empty lemmas at the base; usually imported.

P. arundinacea L., **reed canary grass**, is a coarse perennial of wet places, creeping by rhizomes. It has a much larger, irregular, slightly-spreading panicle, with smaller spikelets and seed, and hairy empty lemmas. Common in wet lowland conditions in Britain, dying down

to ground-level in winter, and not considered of agricultural value here, but sown on wet land in the U.S.A., where a number of cultivars have been developed.

Phalaris tuberosa L. is a species of Mediterranean origin, but developed and much cultivated in Australia and other warm areas. It is a large glabrous perennial with broad succulent leaves, somewhat resembling timothy in appearance, making considerable growth in winter, but insufficiently hardy for use in Britain. Readily identified by the anthocyanin in the sap of the leaf-sheaths—young shoots 'bleed' when crushed; and by the stout cylindrical panicle, intermediate in appearance between *P. canariensis* and *P. arundinacea.* A hybrid (S 230) with the latter species was produced at Aberystwyth, which successfully combined the winter greenness of *P. tuberosa* with some of the hardiness of *P. arundinacea,* but which proved to be of too low digestibility to be of value.

AGROSTIDEAE

AGROSTIS. BENT GRASSES

Inflorescence a spreading panicle, spikelets one-flowered, small; glumes narrow, pointed; 'seed' very small, consisting of caryopsis enclosed in small palea and round-backed awnless or dorsally-awned lemma; rachilla not usually continued above lemma base.

Several similar species, each showing considerable variation, are commonly found in Britain. All are grasses of low agricultural value, some useful under hill-grazing conditions, but all, under lowland conditions, are important primarily as weeds, mainly in grassland, but sometimes in arable. They are therefore conveniently considered together.

Inflorescence. A delicate, more or less spreading panicle, with slender branches. Spikelets one-flowered, very small, *c.* 3 mm.

'Seed'. The smallest of all British grass 'seeds', usually recognizable on size alone; *c.* 2 mm long, 11–13 million per kg. Round-backed, narrow oval, usually hairless, awned only in *A. canina.* Not sown, except for lawns and sports turf.

Vegetative characters. Perennials, widely-creeping by rhizomes or stolons; low-growing. Leaves rolled in bud, shoots round. Leaf-blades linear, acute, ribbed above, thin, dull. Auricles absent, ligule variable, sheaths split, slender, glabrous, green or sometimes reddish (illustration p. 202).

Agricultural importance. The bents are all relatively low yielding grasses, with a large proportion of creeping stem, starting growth late in spring. Under good conditions, creeping bent has been recorded as giving about three-quarters of the dry matter yield of perennial ryegrass, but the digestibility is lower, and the useful productivity has been estimated as rather under 70% of that of ryegrass. The growing season is relatively short but yield during this period fairly even. Bents are very tolerant of low fertility, and show comparatively small responses to added nitrogen. Being extensively creeping, they can spread rapidly when once established. Invasion by bent grasses is thus one of the commonest causes of degeneration of leys. Control of established bent is not easy. Bents are relatively susceptible to low concentrations of paraquat and dalapon, and selective control by these herbicides may be possible, but usually a bent-infested ley will be regarded as ready for ploughing.

The larger and coarser forms of bent, particularly those with well-developed rhizomes, may become arable weeds. Although they are not usually as serious a problem in arable crops as couch, it must be remembered that they, unlike couch, are also capable of persisting and spreading in grassland. It is very important, therefore, that arable land overrun with bent should be thoroughly cleaned before sowing down to a ley.

DISTINCTION BETWEEN DIFFERENT AGROSTIS SPECIES

Agrostis stolonifera L. **Creeping Bent,** Fiorin.
Stoloniferous, panicle closely contracted in fruit, lemmas awnless; ligule long, rounded; tetraploid. The commonest species in lowland grassland, especially where damp; occasional as an arable weed. Some of the finer-leaved forms may be used for lawns; four cultivars included in 1977 United Kingdom national list.

Agrostis gigantea Roth. **Black Bent, Red-top**
Rhizomatous, panicle large, always spreading, lemmas awnless; leaves broad, coarse, ligule long, blunt; hexaploid. Mainly an arable weed; occasional in damp grassland. Sown in U.S.A. on wet acid soils; not used in Britain at all commonly, but one cultivar listed 1977.

Agrostis tenuis Sibth. **Fine Bent, Brown-top**
Short rhizones or stolons, panicle small, always spreading, lemmas awnless; leaf-blades narrow, ligule short, blunt; tetraploid. Common in poor dry grassland, both calcareous and acid; usually the common-

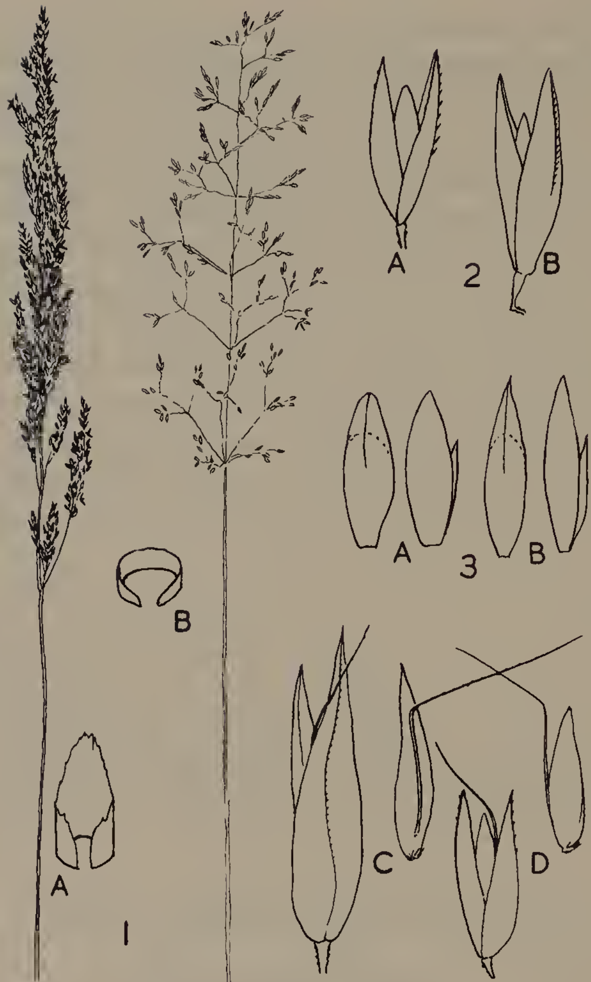


Fig. 69. Bent grasses. 1, panicle, ×½, and diagram of shape of ligule. 2, spikelet, ×10. 3, 'seed', dorsal view, and side view partially separated to show palea, ×10 of A, creeping bent (*Agrostis stolonifera*), and B, fine bent (*A. tenuis*). C, spikelet and 'seed' of bristle bent (*A. setacea*), ×10; D, of velvet bent (*A. canina*).

est species on hills and mountains. The most frequently sown species for fine lawns; eleven cultivars listed 1977.

(Crossing may take place between any of these first three species; hybrids are usually intermediate in character between the parents, and sterile.)

Agrostis canina L. **Velvet Bent**
Panicle small, closing in fruit, lemmas usually awned, palea minute; leaf-blades narrow, ligule pointed. Subsp. *canina,* stoloniferous, diploid, in wet lowland grassland, not common; subsp. *montana* Hartm. rhizomatous, tetraploid, frequent in dry hill pasture, sometimes used for lawns. Two cultivars of this species listed 1977.

A. setacea Curt., bristle bent, is a very distinct plant of acid heath

and moorland in S.W. England; closely-tufted, not creeping, leaves resembling sheep's fescue, panicle slender, lemma awned, palea minute. Negligible agricultural value.

Gastridium ventricosum (Gouan) Schinz & Thell., nitgrass, is an annual somewhat resembling *Agrostis,* but with dense panicle and glumes longer and swollen at base. Occasionally found as arable weed in S. England.

Ammophila arenaria (L.) Link., marram grass, is a much larger grass with large, dense panicle, very stout rhizomes and large, stiff, inrolled leaves. A valuable sand-binding grass, often planted (not sown) to prevent movement of sea-coast dunes.

PHLEUM. TIMOTHY OR CAT'S-TAIL

Panicles dense, spike-like, cylindrical; spikelets one-flowered; glumes equal, stiff, keeled; lemma short, blunt, awnless.

Phleum pratense L. **Timothy**

A high-yielding, palatable perennial for moist conditions, important and frequently sown in leys.

Inflorescence. Dense, cylindrical, spike-like panicle, up to 15 cm long; spikelets *c.* 3 mm, with glumes square-topped, but keel extended as long, stiff, awn-like point; keel fringed with stiff hairs. The single floret is only about half the length of the glumes and completely hidden by them.

'Seed'. The single floret threshes out of the glumes, and the 'seed' thus consists of the caryopsis enclosed in the thin, blunt, oval, silvery lemma and palea. No rachilla is present. The 'seed' is shorter and rounder (*c.* 2 mm) than most grass 'seed', running freely and readily cleaned; 2·2 million per kg. The lemma and palea are rather readily rubbed off, exposing the brown pericarp, and most seed samples contain a proportion of such 'brown seed'; germination is not affected by this shelling-out, and the presence of 'brown seed' is no disadvantage, except for seed that is to be stored for some years, although a very large percentage in a sample may be an indication of old or badly-machined seed.

Vegetative characters. A large, tufted, glabrous, rather succulent

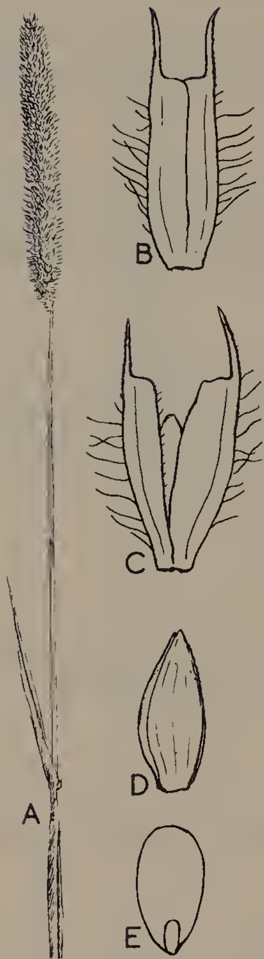


Fig. 70. Timothy, *Phleum pratense*. A, panicle, ×½. B, spikelet, ×7. C, the same with glumes separated to expose 'seed'. D, 'seed' usual state with caryopsis enclosed in lemma and palea, ×10. E, 'brown seed' state, caryopsis only, ×10.

perennial. Leaves rolled in bud, shoots round. Leaf-blades broadest near middle, thick in texture, ribbed above, light grey-green. Auricles absent, ligule short obtusely-pointed; sheaths split, not keeled, usually pale. Base of tillers often bulbous, due to formation of haplocorm, i.e. swollen lowest internode (illustration p. 202).

Agricultural importance. Timothy is a high yielding palatable grass for moist soils of medium or high fertility. Its useful productivity has been estimated as 83% of that of perennial ryegrass; under good conditions the total annual dry matter yield is about 9 000 kg/ha under a nine cut regime and up to 12 000 with four cuts. Digestibility falls markedly well before ear emergence, but this takes place relatively late, and a first conservation cut at 66 D-value of some 4 500 kg/ha can be taken at the end of May or early in June. Spring growth starts rather late, but production is well maintained during the sum-

mer, and timothy can thus be regarded as complementing perennial ryegrass, in the production of which there is often a summer depression. The two are frequently sown together on the moister soils, but timothy is much less aggressive in the young plant stage, and its establishment in such mixtures may be low, particularly if grazing is hard. The lack of aggressiveness of timothy makes it a satisfactory companion to meadow fescue, and the two species may form the basis of non-ryegrass leys.

Origin. Timothy as usually grown is a hexaploid with forty-two chromosomes in the somatic cells. Its origin is not entirely clear; it has been variously interpreted as an allopolyploid derived from a cross between the diploid *P. bertolonii* DC. (see below p. 190) and the tetraploid form of *P. alpinum* L., which in Britain is found only in the mountains of northern England and Scotland, or as an autopolyploid derived from *P. bertolonii* only. There seems no doubt that it was first recognized as a grass of agricultural merit in North America, being first recorded in New Hampshire, and later introduced into Maryland by a farmer named Timothy Hansen about 1720. Introduced into England with the name 'timothy' in 1760, and shortly afterwards into continental Europe, its good characters were quickly appreciated, and it came into general cultivation. If it is an allopolyploid it could well have originated in the seventeenth century in North America, where *P. alpinum* is widespread and *P. bertolonii* introduced from England, and thus have been a new species when first recorded. If it is an autopolyploid it is perhaps more likely to have originated in Europe at some unknown date, its agricultural value not being recognized until it was accidently introduced into America. The question, which has been complicated by differences in the nomenclature used by different authorities, must remain an open one.

Cultivars. The erect rather stemmy commercial timothy used during the early twentieth century has been superseded by bred cultivars, but the local Scots variety has remained in use. This and Aberystwyth S 352, less persistent but with a longer growing season, are early varieties heading near the beginning of June, and outyielding later heading cultivars under a four-cut regime. Aberystwyth S 51, a distinct form with long rather yellow-green leaves, is medium late heading, but not later in starting growth. Aberystwyth S 48 is a persistent late timothy; a number of cultivars from France, Sweden and the Netherlands are also available. A total of 39 cultivars were listed in 1978/9.

Phleum bertolonii DC. (*P. nodosum* auct.). **Small Timothy, Cat's-tail**

This diploid species is similar to the hexaploid timothy, but much lower-growing, with smaller panicle and narrower leaves, and slightly smaller 'seed'. It is strongly-creeping, with spreading stems below and above ground, and distinctly more drought-resistant than large timothy. It is found commonly in well-grazed pastures on rather thin soils, such as the lower hill pastures of fairly high fertility. Very persistent under grazing, but not high-yielding. The diploid and hexaploid timothy species do not usually cross with each other.

Aberystwyth S 50 was one of two cultivars listed in 1978/9 which were designed for agricultural use; it would be used for long grazing leys and permanent pasture mixtures only, as its comparatively low yield and rhizomatous growth make it unsuitable for short leys. The seed yield is low, and the seed price tends to be high. This species can also be used for non-agricultural swards, and three cultivars were listed in 1978/9 for amenity purposes.

ALOPECURUS. FOXTAIL GRASSES

Alopecurus differs from *Phleum* in its softer glumes usually joined at the base and shed as part of the 'seed', and in the lemma being awned, and palea and lodicules absent, flowers protogynous.

Alopecurus pratensis L. **Meadow Foxtail**

A palatable early grass of moist, old grassland, rarely sown in leys.

Inflorescence. A dense, spike-like panicle 5–10 cm long, more tapering than that of timothy. Spikelets ovate, flat, hairy, *c.* 5 mm, consisting of a pair of equal keeled glumes, joined at base, and enclosing a single floret. Lemma with long, almost basal awn, extending well beyond tip of glumes.

'Seed'. The whole spikelet drops entire; the 'seed' is thus large, *c.* 5 mm, but light, about 1·6 million per kg, hairy and awned, and thus of a type difficult to clean satisfactorily, not flowing readily over sieves, and with empty spikelets, in which the caryopsis has failed to develop, difficult to separate from full ones.

Vegetative characters. A loosely-tufted, rather large perennial spreading slightly by very short rhizomes. Leaves rolled in bud, shoot round, glabrous. Leaf-blades long, dark green, ribbed above, dull

below. Auricles absent, ligule medium length, square-topped; sheaths split, somewhat ribbed, base of old sheaths becoming dull purplish-brown (illustration p. 202).

Agricultural importance. A palatable, moderately high-yielding, very early perennial of moist grassland of medium to high fertility; not very tolerant of hard spring grazing and found more commonly in fields used mainly for hay. For this purpose and type of land it is a valuable grass, and to be welcomed when it volunteers in old grassland, but the difficulties involved in establishing it largely preclude its use in leys. Not only is the 'seed' difficult to clean, and therefore usually of low germination and purity, but the percentage establishment is low, *c.* 20% and seedlings grow slowly and suffer severely in competition with other more aggressive plants. Meadow foxtail rarely makes much contribution to the sward if included in a mixed ley; in the U.S.A., where it is of rather greater importance, it is usually sown alone. A further disadvantage is that seed production in

Fig. 71. Foxtail grasses. 1, panicle, $\times\frac{1}{2}$. 2, 'seed' (whole spikelet), $\times 10$, of A, meadow foxtail (*Alopecurus pratensis*), and B, slender foxtail (*A. myosuroides*). C, fertile tiller and panicle of floating foxtail (*A. geniculatus*), $\times\frac{1}{2}$.

Britain presents considerable difficulties, mainly owing to attack by gall midges.

Alopecurus geniculatus L., floating foxtail, is a small, shortly-creeping perennial of very wet lowland grassland, with culms conspicuously angled at the nodes (geniculate=kneed) and small greyish cylindrical panicles *c.* 3 cm long in May. Palatable, but too low in yield to be of any real value. Hybrids with *A. pratensis* exist.

Alopecurus myosuroides Huds. (*A. agrestis* L.), **slender foxtail, black grass**, is an annual arable weed, usually germinating in autumn, and forming a compact tuft of narrow leaves with panicles up to about 50 cm high in May and June. The panicles are considerably more slender than those of meadow foxtail, with relatively few large, oblong spikelets, and setting abundant seed. The 'seed' is the whole spikelet, similar to that of meadow foxtail in structure, but narrower, heavier and almost hairless.

Slender foxtail is rather local in its distribution, but in those areas where it is prevalent it is, on heavy soils, one of the most serious weed grasses, its abundant early seeding before cereals are fit to harvest resulting in very heavy contamination of the soil. Seedling growth is rapid, and black grass infestation of a cereal crop can cause a serious drop in the yield potential at a very early stage. Pre-emergence or early post-emergence spraying with herbicides such as chlortoluron, methabenzthiazuron or an isoproturon is therefore desirable. In root crops or fallow black grass is readily controlled by cultivations; seed does not normally remain dormant in the soil for more than two years.

Black grass is not an important weed of grazed grassland, but it may persist in grass seed crops, and be an impurity of ryegrass and fescue. It is therefore subject to special rules under the 1976 regulations for fodder plant seeds, and also under those for oil and fibre plant seeds.

GLYCERIEAE

Glyceria is a genus with an inflorescence of the festucoid type, with lax, cylindrical spikelets and very blunt, round-backed lemmas; it differs, however, in its small chromosomes and connate lodicules and has therefore been referred to a separate tribe. *Glyceria fluitans* (L.) R.Br., **floating sweet-grass**, has slender panicles and vegetative characters resembling those of a much-enlarged, very succulent, rough-stalked meadow-grass. This, and some related species and hybrids, are common and palatable grasses of water-meadows, riversides and very wet lowland grassland, where they may provide useful

Fig. 72. Floating sweet-grass, *Glyceria fluitans*. A, panicle, ×½. B, leaves, × ½. C, base of stem, × ½. D, spikelet, ×¾.

herbage. *Glyceria maxima* (Hartm.) Holmb., reed meadow-grass, has large spreading panicles, stout rhizomes and upright shoots forming large clumps.

NARDEAE

Nardus stricta L., **mat grass**, is a common perennial of mountain and moorland, not closely related to other British grasses. It has a one-sided spike (*c.* 30 cm high) with one single-flowered spikelet at each node; the glumes are reduced to minute scales at the base of the sharply-pointed lemma. Style single, no lodicules, protogynous.

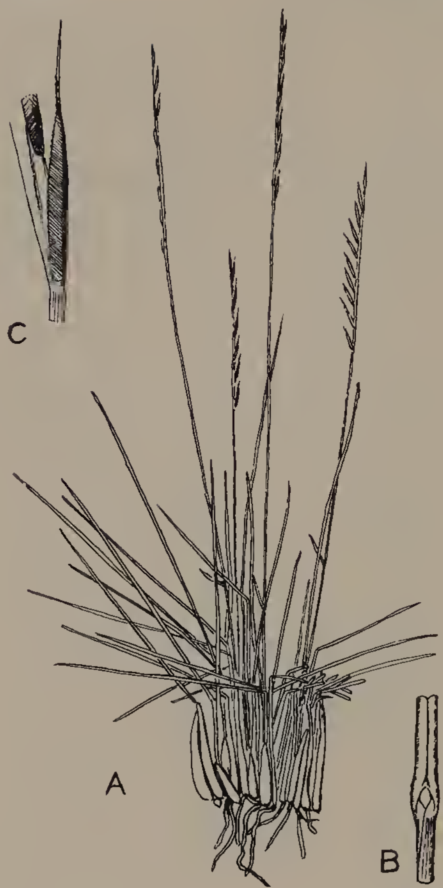


Fig. 73. Mat-grass, *Nardus stricta*. A, plant showing tufted habit, ×½. B, ligule and base of rolled leaf blade, ×3. C, spikelet, × 4.

Nardus forms densely-packed tufts, with tough, persistent sheaths, making tillers stiff, comb-like; leaf-blades bristle-like, very wiry. Plant rather pale grey-green, leaves dying off almost white. Often abundant in almost pure stand on damp thin peat. Annual dry matter yields of about 1 000 kg/ha have been recorded for *Nardus* grassland, but the herbage is of very low palatability, and is usually rejected by sheep when any other vegetation is available. It does however provide some winter keep by sheep eating the partially cured dormant herbage when no alternative remains. Nardus is moderately resistant to hard grazing and to burning, but susceptible to low concentrations of dalapon.

DANTHONIEAE

Molinia caerulea (L.) Moench, called purple moor grass, but usually known by its generic name, is a large tufted perennial of wet peat. The inflorescence is a rather narrow panicle *c.* 1 m high, with few-flowered spikelets *c.* 6 mm long, often purplish in colour; anthers and

Fig. 74. Purple moor-grass, *Molinia caerulea.* A, flowering shoot, ×¼. B, swollen base of stem, ×½. C, spikelet, ×2.

stigmas purple. Culms with very long upper internode, and lower part swollen. Leaves, thin, dry, dying off brown in winter and blades deciduous. Ligule replaced by a fringe of hairs.

A very common plant of deep wet peat, often dominant on mountain grassland; palatable only in extremely young stage and thus of very low grazing value. Annual dry matter yields may be up to 1 500 kg/ha, but the herbage is of low digestibility and difficult to utilize. Molinia is resistant to burning, but susceptible to hard grazing by sheep, if this can be achieved; it is also susceptible to low concentrations of dalapon or paraquat.

Sieglingia decumbens (L.) Bernh. *(Triodia decumbens* (L.) Beauv.), heath grass, more commonly known as triodia, has a smaller panicle than *Molinia,* with longer glumes and three-cleft, blunt tip to

Fig. 75. Heath grass, *Sieglingia decumbens.* A, panicle, $\times\frac{1}{2}$. B, spikelet, $\times 3$. C, 'seed', ventral view, $\times 10$.

lemmas; flowers cleistogamous. A tufted perennial, smaller than molinia, common in mountain grassland but rarely in any great quantity. Fairly palatable and usually kept well grazed down.

ARUNDINEAE

Phragmites australis (Cav.) Steud. (*P. communis* Trin.). **Common Reed**

Common in shallow water in Britain fringing rivers and lakes and forming reed swamps. Perennial with stout rhizomes and erect aerial stems up to 2 m, leaves broad, stiff, panicles large, with numerous few-flowered spikelets with long silky hairs. Of no grazing value, but used as thatching material (Norfolk reed).

Cortaderia selloana (Schult.) Asch. & Graeb., pampas grass, with very large shoots and conspicuous decorative panicles, South American, is often planted for ornament.

CHLORIDEAE

Spartina anglica Hubb. **Common Cordgrass**

A perennial of coastal mudbanks; inflorescence a branched spike of one-flowered spikelets. An amphidiploid derived by chromosome

doubling from a cross between the smaller diploid species *S. stricta* Roth. and the introduced American *S. alterniflora* Lois. The name *S.* × *townsendii* Groves refers strictly to the original sterile diploid hybrid only, but has been commonly used also for the fertile tetraploid. The tetraploid is much more vigorous than either parent and is capable of growing in sea water and building up mudbanks which eventually form dry land; widely planted around the British coasts for this purpose. Not good grazing, but can eventually be replaced by better species. (Sometimes referred to a separate tribe *Spartineae.*)

Cynodon dactylon (L.) Pers. **Bermuda Grass**

A perennial creeping by means of rhizomes and stolons, ligule replaced by a ring of hairs, inflorescence a digitately branched spike, branches spreading with numerous short rounded one-flowered spikelets. A rare and unimportant sea coast plant in southern England, dying down to ground level in winter. Widespread in warm and subtropical areas, colonizing disturbed ground and a useful herbage plant and lawn grass.

Chloris gayana Kunth., Rhodes grass, is an important tropical herbage grass; species of *Bouteloua* and *Buchloe* are useful indigenous grasses in North America.

BAMBUSEAE

The *Bambuseae* includes the woody bamboos, mainly subtropical, of considerable economic, but no agricultural importance. Some species of *Arundinaria*, *Pseudosasa* and other genera are grown in Britain for ornament and are occasionally utilized as a source of canes for horticultural uses.

PANICEAE

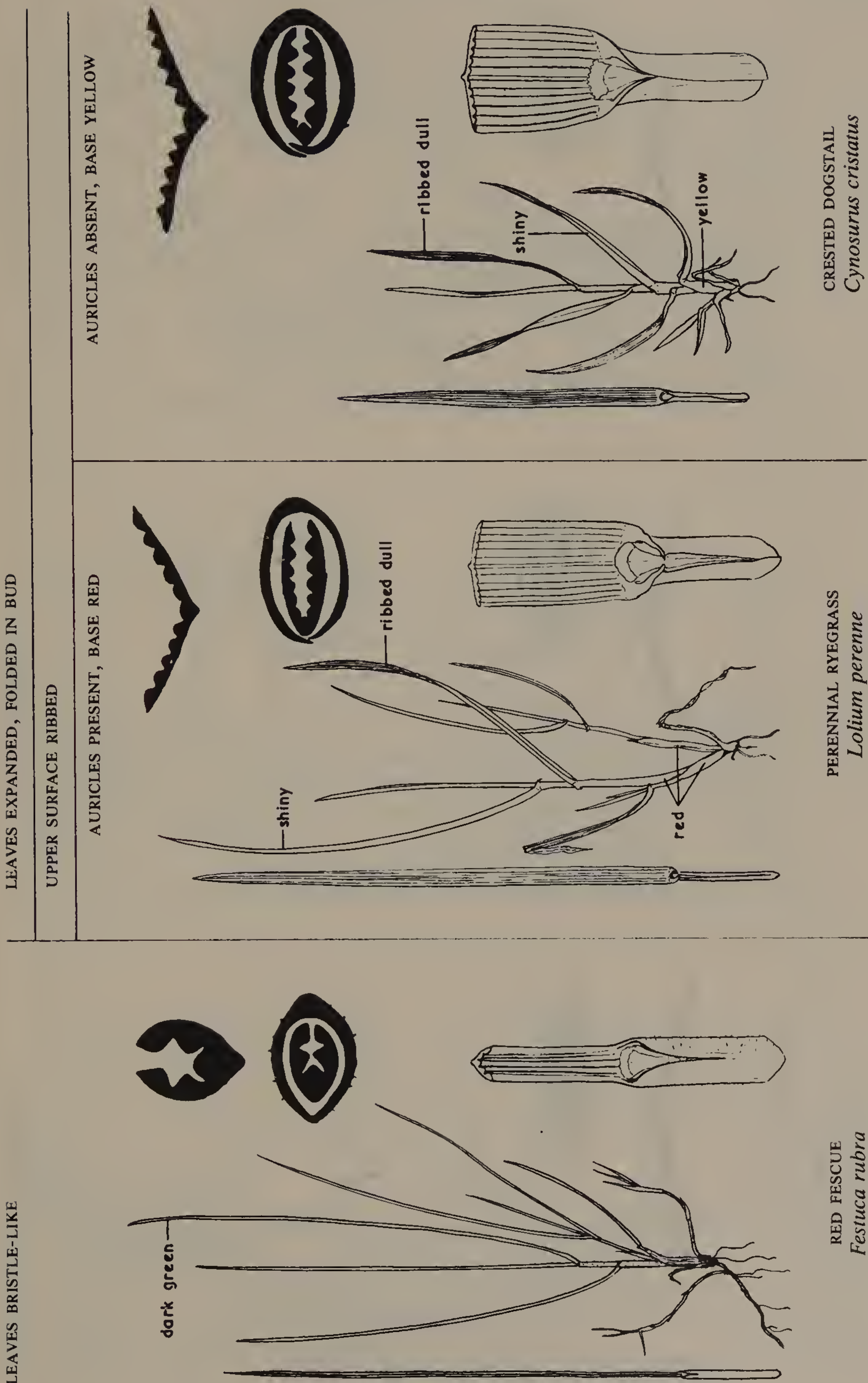
The *Paniceae* includes a number of warm-climate annuals such as *Echinochloa crus-galli* (L.) Beauv., *Digitaria sanguinalis* (L.) Scop., *Setaria viridis* (L.) Beauv. and *S. glauca* (L.) Beauv. which are unimportant casuals in Britain. In tropical areas the tribe provides numerous important herbage grasses such as *Setaria anceps* Stapf, *Panicum maximum* Jacq. (Guinea grass) and *P. barbadense* Trin. (Para grass), *Pennisetum purpureum* Schum. (elephant grass and Napier grass) and *Paspalum dilatatum* Poir.

ANDROPOGONEAE

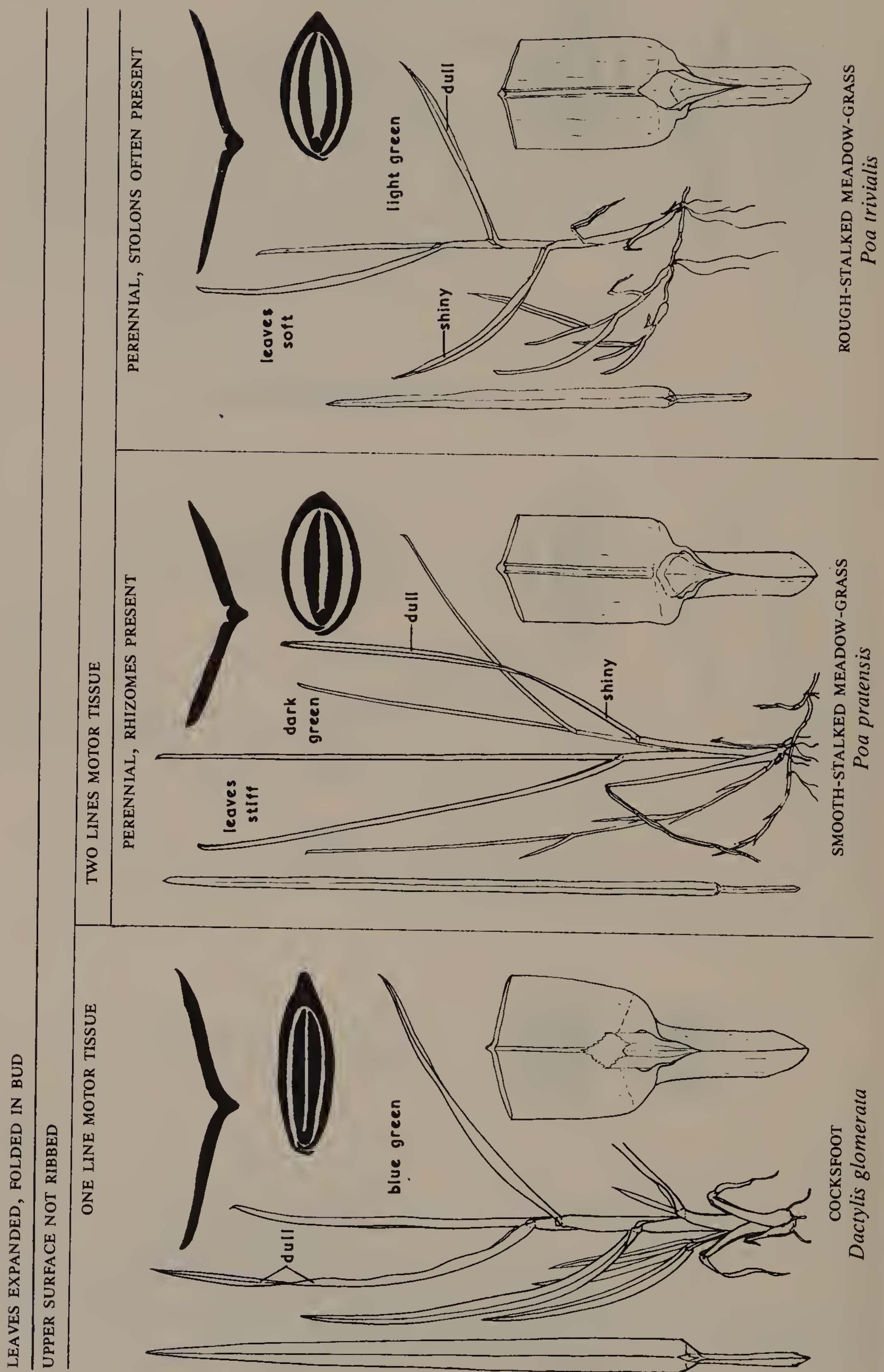
There are no British representatives of the tribe *Andropogoneae*, but a number are important tropical grasses; these include *Sorghum sudanense* Stapf. (Sudan grass), *S. halepense* (L.) Pers. (Johnson grass, useful grazing but also capable of spreading as a serious arable weed) and species of *Andropogon, Hyparrhenia* and *Themeda.*

Illustrated Key for Identification of Common Grasses in Vegetative Stage

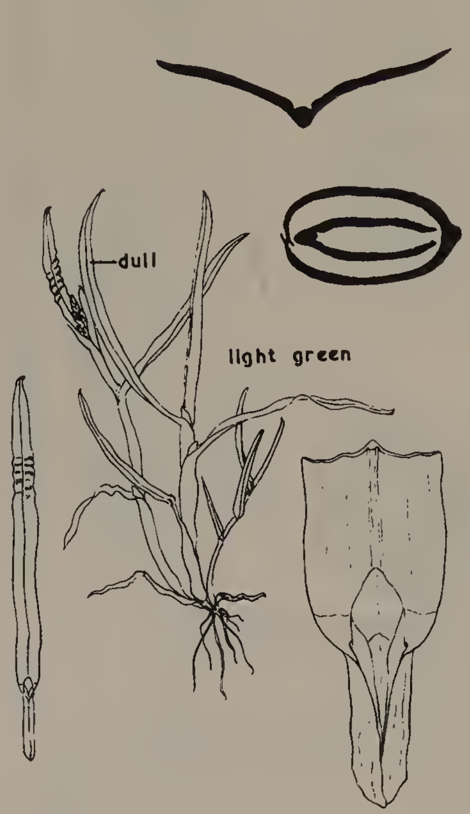
The key includes only the species most commonly found as constituents of lowland grassland swards. The illustrations for each species include a single vegetative tiller, or a group of tillers; a single leaf; an enlarged view of the junction of leaf-sheath and blade; and diagrammatic transverse sections of leaf-blade and shoot.



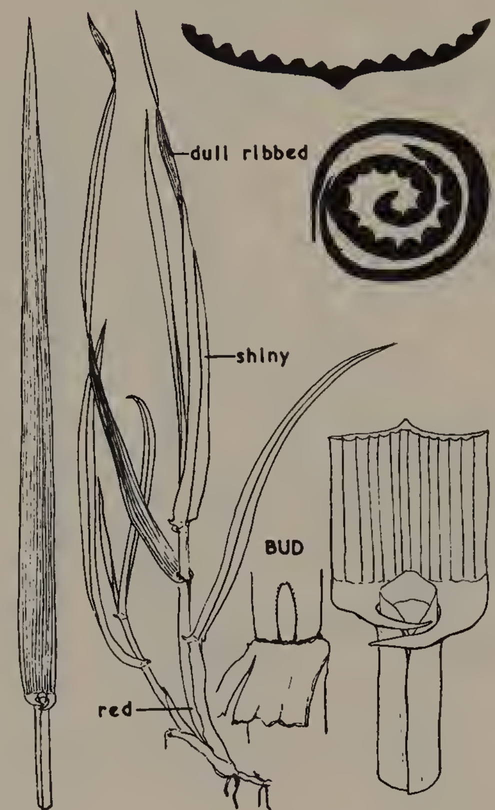
LEAVES BRISTLE-LIKE
dark green
RED FESCUE
Festuca rubra
LEAVES EXPANDED, FOLDED IN BUD
UPPER SURFACE RIBBED
AURICLES PRESENT, BASE RED
shiny
ribbed dull
red
PERENNIAL RYEGRASS
Lolium perenne
AURICLES ABSENT, BASE YELLOW
ribbed dull
shiny
yellow
CRESTED DOGSTAIL
Cynosurus cristatus


LEAVES EXPANDED, FOLDED IN BUD
UPPER SURFACE NOT RIBBED
ONE LINE MOTOR TISSUE
TWO LINES MOTOR TISSUE
PERENNIAL, RHIZOMES PRESENT
PERENNIAL, STOLONS OFTEN PRESENT
dull
blue green
COCKSFOOT
Dactylis glomerata
leaves stiff
dark green
dull
shiny
SMOOTH-STALKED MEADOW-GRASS
Poa pratensis
leaves soft
shiny
light green
dull
ROUGH-STALKED MEADOW-GRASS
Poa trivialis

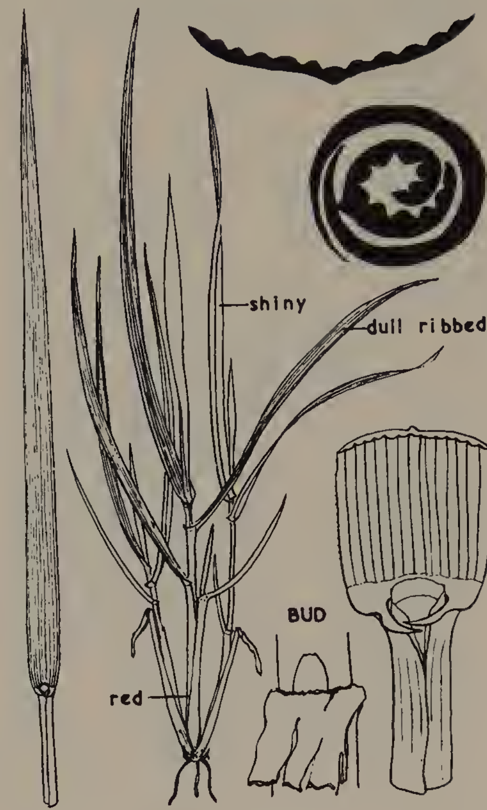
LEAVES EXPANDED, FOLDED IN BUD	LEAVES EXPANDED, ROLLED IN BUD	
UPPER SURFACE NOT RIBBED	GLABROUS	
TWO LINES MOTOR TISSUE	AURICLES PRESENT	
ANNUAL, TUFTED	OLD SHEATHS WITHERING	OLD SHEATHS PERSISTENT, TOUGH



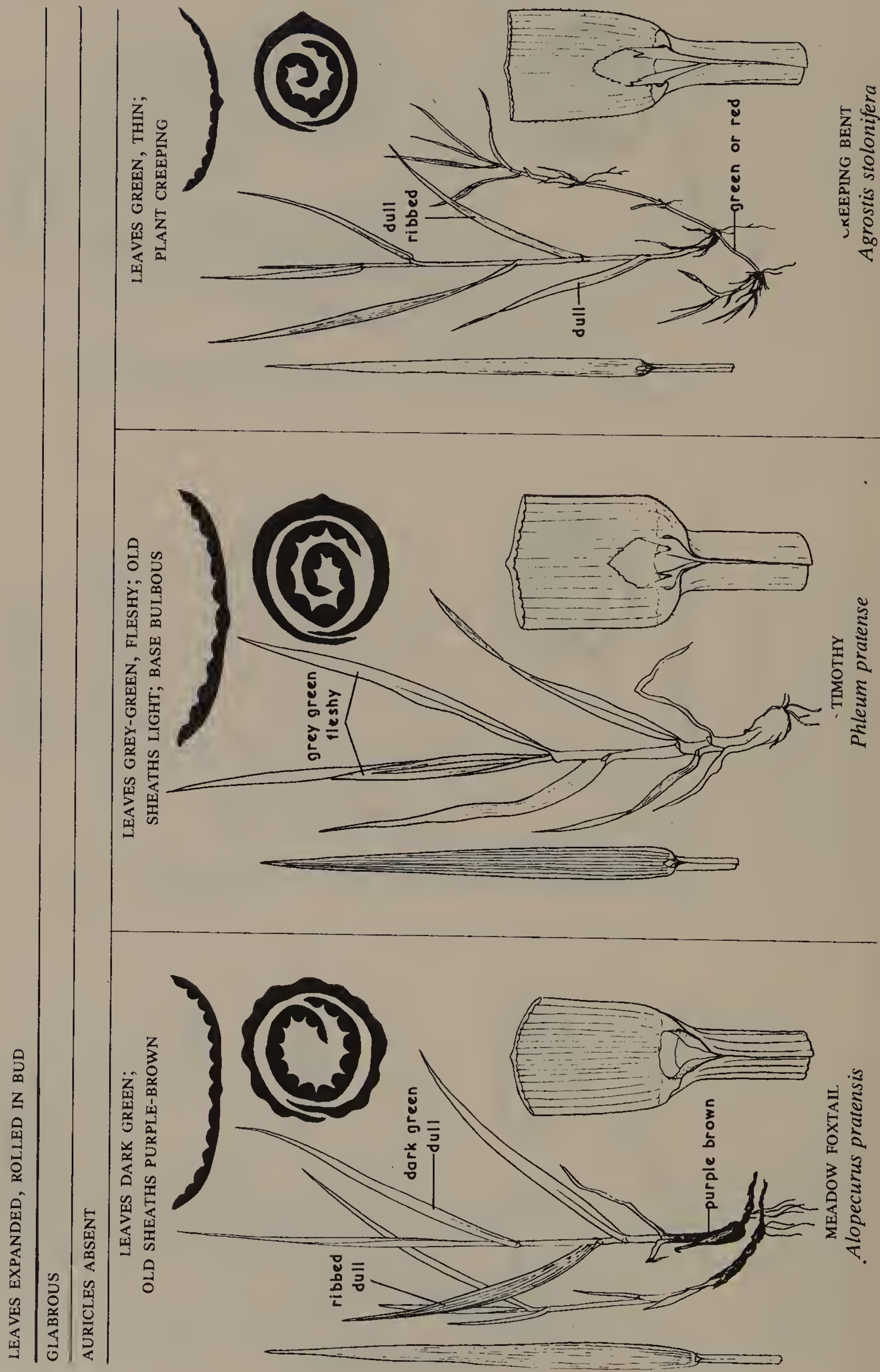
ANNUAL MEADOW-GRASS
Poa annua



ITALIAN RYEGRASS
Lolium multiflorum



MEADOW FESCUE
Festuca pratensis


LEAVES EXPANDED, ROLLED IN BUD
GLABROUS
AURICLES ABSENT
LEAVES DARK GREEN; OLD SHEATHS PURPLE-BROWN
ribbed
dull
dark green
dull
purple brown
MEADOW FOXTAIL
Alopecurus pratensis
LEAVES GREY-GREEN, FLESHY; OLD SHEATHS LIGHT; BASE BULBOUS
grey green
fleshy
TIMOTHY
Phleum pratense
LEAVES GREEN, THIN; PLANT CREEPING
dull
ribbed
dull
green or red
CREEPING BENT
Agrostis stolonifera

LEAVES EXPANDED, ROLLED IN BUD

HAIRY

AURICLES PRESENT

COUCH
Agropyron repens

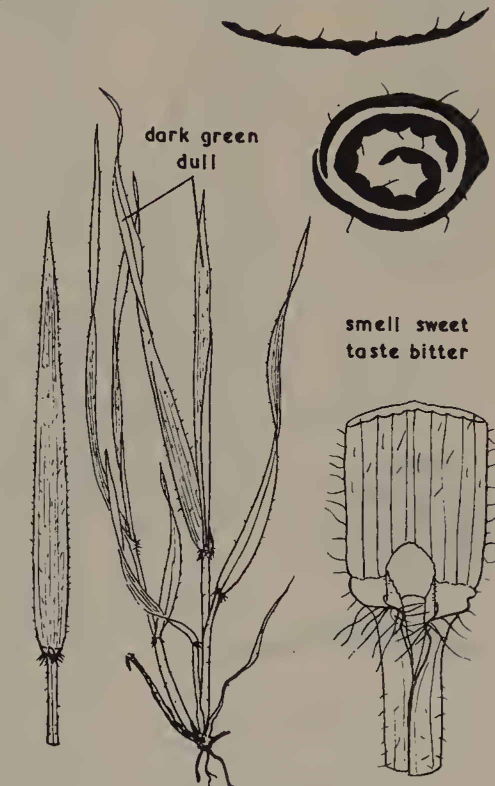
AURICLES ABSENT

SHEATH OPEN

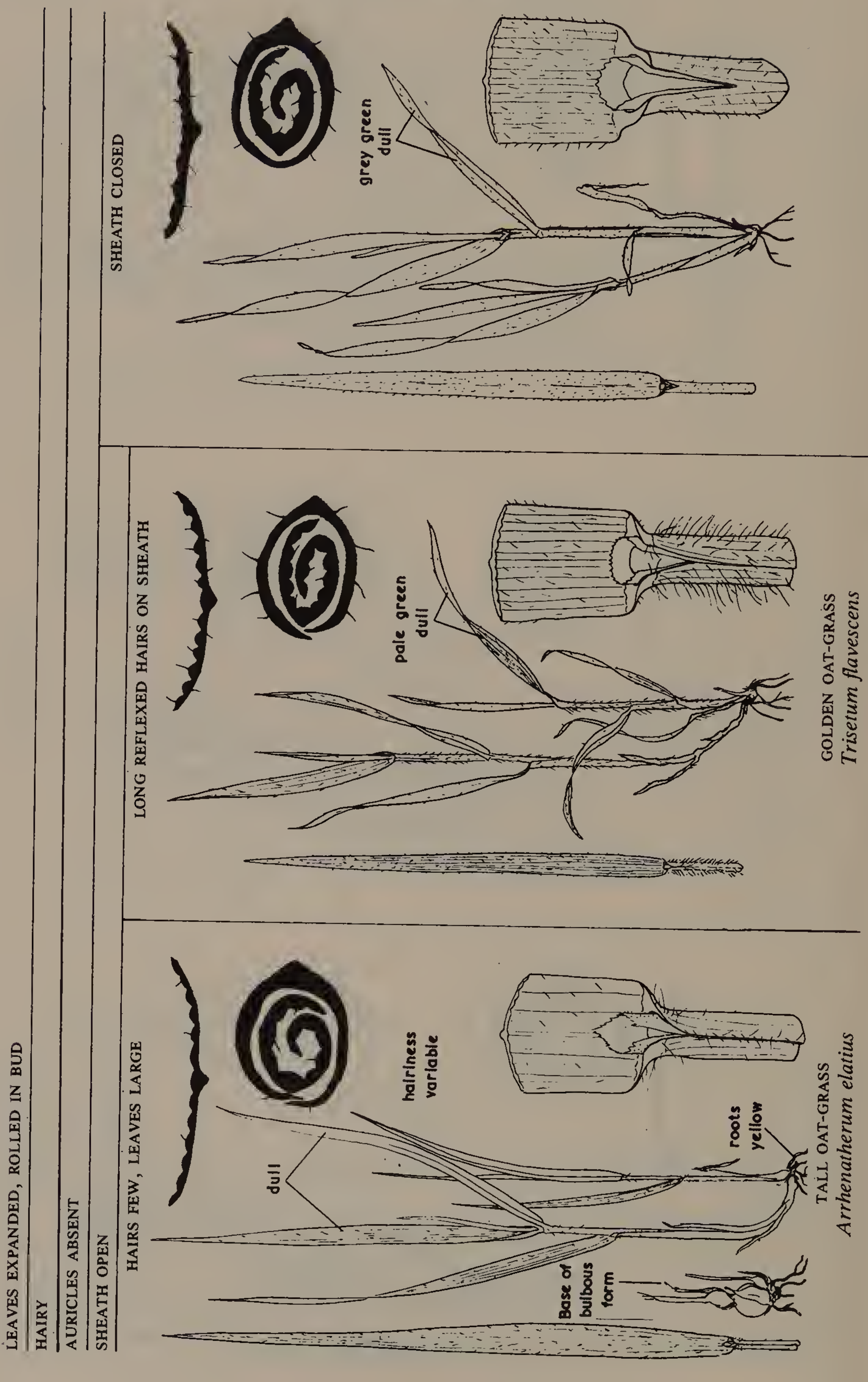
SHEATH RED-VEINED

YORKSHIRE FOG
Holcus lanatus

TUFT OF LONG HAIRS AT BASE OF LEAF-BLADE



SWEET VERNAL-GRASS
Anthoxanthum odoratum


LEAVES EXPANDED, ROLLED IN BUD
HAIRY
AURICLES ABSENT
SHEATH OPEN
HAIRS FEW, LEAVES LARGE
dull
hairiness variable
roots yellow
Base of bulbous form
TALL OAT-GRASS
Arrhenatherum elatius
LONG REFLEXED HAIRS ON SHEATH
pale green dull
GOLDEN OAT-GRASS
Trisetum flavescens
SHEATH CLOSED
grey green dull

8

GRASSLAND

TYPES OF VEGETATION

The type of natural vegetation in any area depends partly on climatic conditions, partly on soil conditions and partly on biotic conditions. Biotic conditions are those produced by other organisms, and here the effects of grazing animals are particularly important. Grasses show a very wide range of adaptability to different climatic and soil conditions, and, as has been pointed out in discussing their mode of growth, are usually very tolerant of grazing. Their usually low growth, with vegetative stems and buds at or near ground-level, while making them resistant to damage by grazing, at the same time makes them susceptible to shading-out by taller-growing plants. Grassland is consequently only found where conditions do not allow the establishment of a dense cover of shrubs or trees. The main natural grassland areas of prairie and steppe occur where conditions are too dry for tree growth, but all gradations exist from semi-desert through grassland with scattered trees to open woodland. Mountain grassland also occurs above the level of tree growth. In these cases, grassland is the ecological climax, and does not tend to be replaced by other types of vegetation. In other areas, however, grassland is not the climax, and is only found because the woodland climax vegetation is prevented from establishing itself. This is true of almost all grasslands in Britain except the mountain areas; in Britain the natural climax is forest, and grassland originated by progressive clearance of forest from neolithic times onward, and is maintained as such by grazing preventing the normal succession through bushes and scrub to woodland again.

TYPES OF GRASSLAND

Grassland can thus be divided into three types: natural, semi-natural and cultivated. True natural grassland is, as has been said, of limited occurrence in Britain, and even those areas where it is a true climax are considerably influenced by grazing. Semi-natural grasslands in Britain include rough grazing and hill land, where the vegetation

reflects largely the climatic and soil conditions modified only by the effect of the grazing animal, and in some areas by periodic burning. Cultivated grassland is more directly controlled by the farmer; not only is grazing more precisely managed, but soil conditions can be altered by manuring and drainage, and at least in temporary leys the main species present can be decided by choice of seeds mixture. Clearly no hard and fast line can be drawn between these types, and old pasture, even although originally sown, may be regarded as semi-natural if it receives little attention. The plants present in such old pastures reflect the climatic and soil conditions and the effect of grazing, and may bear little relation to the species originally sown.

The greater part of the grassland of Britain, other than short leys, can thus be regarded as semi-natural, in that, although maintained as grassland mainly by grazing, the composition of the sward is determined largely by climate (here mainly a function of height above sea-level) and soil.

Some five-and-a-half million hectares are described in the official returns to the Ministry of Agriculture as cultivated grassland, and about one and three-quarter millions as rough grazings. Of the cultivated grassland, about four million hectares is described as permanent pasture, and the remainder as temporary grassland. This distinction is however an arbitrary one, often more influenced by tradition or intention than by any real differences in history or sward composition. A more useful division is into 'sown grass', including the temporary grassland and that part of the permanent pasture which has been recently enough sown for the seeds mixture employed to be still an important factor in determining sward composition; and 'old grass' consisting of the remainder of the permanent pasture. This 'old grass' has been estimated* at some 2·8 million ha, and consists of grassland which has never been ploughed, or which was last seeded down so long ago that its composition is determined by climatic, soil and management conditions and not by the seeds mixture used.

Old grass. Some 90% of this old grass area is lowland grassland up to about 300 m. Approximately 20% contains appreciable ryegrass (i.e. 15% or more of the ground cover consists of ryegrass), but it is only under the very best conditions that ryegrass is the dominant species. Such first-class old ryegrass pastures occur only on highly fertile moist soils where management is good and white clover abundant. Under rather poorer conditions bent usually forms a major constituent of the sward, and some 75% of the old grass area is *Agrostis* dominant, with ryegrass forming less than 15% of the plant

* Idle, A. A. *Journal of the British Grassland Society,* **30**, 1975, pp. 111–20.

cover. Cocksfoot, timothy, the larger fescues and the meadow-grasses may be associated with the bent and ryegrass of the better swards. Under poor conditions ryegrass is absent, and the bent accompanied by Yorkshire fog, crested dogstail and sweet vernal. In wet areas of high fertility meadow foxtail and *Glyceria* species may be important; poorer wet areas are dominated by bent and rushes.

The remaining 10% of the old grass area can be described as upland grassland. Some 7·5% is dominated by small fescues. A small part of this fescue grassland is on basic soils; the remaining old grassland of the chalk downs, much reduced in area by arable cultivation since the 1940s, is an example. Downs are chalk or limestone uplands with fairly low rainfall. The porous subsoil results in relatively rapid leaching, the soils are thin and the level of available nitrogen very low, but the general level of fertility is higher than that of the typical hill soils. In addition to small fescues bents are present together with such grasses as golden, meadow and downy oatgrasses and crested dogstail. Small legumes such as birdsfoot trefoil are usually common, as well as a large range of other dicotyledons. In less well-grazed areas the unpalatable tor grass and upright brome may become dominant.

The remainder of the fescue grassland is of very different type, occupying hills and the lower mountain slopes on acid soils. *Agrostis* is usually abundant, but the total number of plant species is typically small, and legumes rare or absent. This acid fescue-bent hill grassland merges into nardus-molinia grassland on more peaty soils; this occupies some 2·5% of the cultivated old grass area. The greater part however of these acid hill lands are returned as rough grazings or common land, and are thus excluded from the figures given for old grass. Grazing is usually extensive, and no lime or fertilizer applied; the productivity of these hill grazings is thus low. The better areas are fescue-bent swards, these grasses being partially or wholly replaced by molinia on deep wet peat and by nardus on thin damp peat. Plants other than grasses may be common; on thin relatively dry peat the heathers *Calluna* and *Erica,* and deer-grass (*Trichophorum caespitosum*), with gorse (*Ulex* spp.) on lower slopes, and bracken (*Pteridium aquilinum* (L.) Kuhn) on deeper soils. All these plants, other than bracken, provide some grazing.

Sown grass. There is no marked distinction between the longer types of leys and land sown down with the intention of leaving it as permanent pasture. It is therefore convenient to treat all types of sown grassland together.

In all sown grassland the initial composition is determined by the seeds mixture used. The objective is normally the production of as

large an amount of digestible dry matter as is possible. The choice of species is thus normally limited to those capable of giving the highest yields. Under fertile lowland conditions the highest yielding species is Italian ryegrass, and this will be the choice if its short life is acceptable. If a longer lasting sward is required the first choice will be perennial ryegrass as having the next highest potential yield. If necessary this will be supplemented or replaced by one or more of the species cocksfoot, timothy and meadow fescue, which have slightly lower potential yields. Grasses with maximum potential yields lower than these are not usually sown in Britain; it is considered more economic to sow high yielding species even under unfavourable conditions and on poor soils where they will eventually be replaced by other unsown species.

Of the grass species sown, Italian ryegrass is short-lived and very intolerant of low fertility. Perennial ryegrass, although long-lived, almost as high-yielding, and readily-established, also requires high fertility, is not drought-resistant, and has a rather fixed rhythm of growth. Cocksfoot, timothy and meadow fescue are all somewhat more tolerant of low fertility, and somewhat more adaptable in growth rhythm, but have lower potential yields and are more difficult to establish. Cocksfoot, and to a lesser extent meadow fescue, are resistant to temporary drought; timothy, although not drought-resistant, gives good summer production.

There is thus no one ideal grass for all conditions; moreover different species have different growth rhythms and thus produce their maximum yield at different times of the year. In very favourable conditions it may be possible to use a mixture which maintains high production throughout the entire year; thus in northern New Zealand leys of perennial ryegrass and *Paspalum dilatatum* (*Paniceae,* not hardy in Britain) can be managed so as to give heavy yields of ryegrass during the winter and of *Paspalum* in summer. In Britain, the most that can be done by the use of more than one species is to extend the growing season into earlier spring or later autumn, and to level up the production at different times of the season. A diagrammatic comparison of seasonal productivity of some common species is given in Fig. 76; for more detailed quantitative curves for particular conditions see Haggar.*

Advantage can be taken of the different merits of the different species in one of two ways; either species can be sown in pure stand in different fields, or a number of species may be mixed in a single

* Haggar, R. J., 'The seasonal productivity, quality and response to nitrogen of four indigenous grasses compared with *Lolium perenne*', *Journal of the British Grassland Society,* **31**, 1976, pp. 197–207.

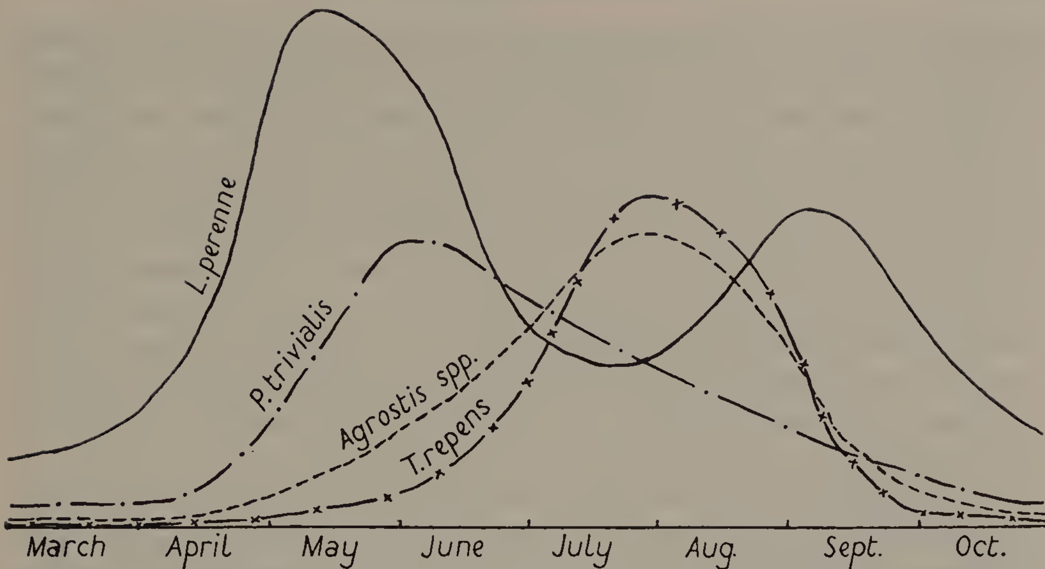


Fig. 76. Variation in the time of maximum growth in different grassland species; diagrammatic seasonal productivity curves for perennial ryegrass, rough-stalked meadow-grass, bent and white clover. From Blackman, G. E., *Emp. J. Expt. Agric.*, **1**, 1933, by permission of the author and the Clarendon Press.

sowing. The former method, that of the ultra-simple seeds mixture, may use one or more cultivars of a single grass species. It has the advantage, at least in theory, that management can be precisely matched to the requirements of the grass, so that maximum production should be attained. For this to be done means however that both field conditions and the requirements of the livestock must be accurately assessed in advance. The alternative arrangement, a general-purpose mixture with two or more grass species included in one sward, is more generally popular. Although it may not give the highest possible yield, in that no system of management will be optimum for all the sward constituents, it is likely to give fairly satisfactory results under a wide range of conditions.

Dicotyledons in sown grassland. It is a common practice to include members of the family *Leguminosae* in sown grassland. They provide highly digestible herbage of high protein and mineral content, and also, by their symbiosis with species of *Rhizobium,* make combined nitrogen available to the grasses. Lucerne (*Medicago sativa*) and sainfoin (*Onobrychis viciifolia*) are high-yielding, but require specialized management and are therefore not suitable for most leys. For these, the choice is almost confined to two clover species. Red clover (*Trifolium pratense*) is a quick-growing biennial or short-lived perennial, forming a rosette in winter but producing erect summer shoots, and used mainly in short leys intended for hay. It is not tolerant of acidity or of very hard grazing, and many cultivars are susceptible to

clover rot and to eelworm damage. It is therefore sometimes replaced or supplemented by the shorter-lived, lower-yielding, but reputedly more resistant alsike (*T. hybridum*). In longer leys the more slowly-establishing but longer-lived white clover (*T. repens*) is commonly included. This is a low growing stoloniferous plant, relatively low yielding at least in the smaller-leaved longer lasting cultivars of the 'wild-white' type, and is grown primarily for its contribution to the nitrogen nutrition of the grasses. Under extensive grazing conditions, where little nitrogen is applied, it is of outstanding value, and its spread can be encouraged, where lime and phosphate supplies are adequate, by hard spring grazing to prevent shading by earlier-growing grasses. Under intensive management, where heavy nitrogen dressings are applied, and long rest periods given, white clover is suppressed, but the relatively small cost of seed is usually considered worth-while in a long ley mixture, even where this type of management is intended.

Dicotyledons other than legumes are usually regarded as weeds in grassland, but there are a number of species which have been recommended as 'grassland herbs' for inclusion either in leys, or in special 'herb-strips' occupying part of the field. The advantage claimed is primarily that their mineral content is higher than that of the grasses; their value however remains controversial, and they have not come into general use. Species recommended have included forage burnet (*Sanguisorba minor* subsp. *muricata*), sheep's parsley (*Petroselinum crispum*), ribwort plantain (*Plantago lanceolata*), yarrow (*Achillea millefolium*) and chicory (*Cichorium intybus*).

DESIGN OF SEEDS MIXTURE

Once the desired type of ley and its composition has been decided on, it is necessary to consider the seeds mixture which will give this type of sward. A number of factors need to be taken into consideration; these include the size of seed, the number of plants required per hectare, the proportion of seeds sown which actually produce a plant, and the effects of competition between plants of the same, and of different, species.

Seed size and weight show considerable variation between the species commonly sown in leys; using approximate figures, the ryegrasses, meadow fescue and red clover have ½ million seeds per kg, cocksfoot 1 million, white clover and alsike 1½ million, and timothy 2 million. Thus a given weight of timothy would contain four times as many seeds as the same weight of ryegrass seed. The proportion of seeds sown which produce a plant capable of surviving depends on

the seed-bed conditions, on the species, and on the rate of sowing. Clearly, if the seed-bed is very poorly prepared, or the weather conditions very unfavourable, very few are likely to become established, but even under good field conditions the number of plants produced is always considerably less than the number of seeds sown. The proportion varies with different species, and may be expressed as the *percentage establishment*; this also varies with the amount sown, and of course with soil and weather conditions. Of the species commonly sown, the ryegrasses, under normal conditions, have a percentage establishment of up to about 60, meadow fescue and cocksfoot about 40, and timothy perhaps 30. Figures for the clovers vary from 30 to 40 but are usually much lower from autumn sowings.

If the seed-rate is increased the percentage establishment decreases; in the original pioneer work at Aberystwyth* the percentage establishment of timothy and perennial ryegrass, each sown as a single grass in mixture with red clover, at different seed rates, was as follows (1 lb/acre = 1·12 kg/ha):

Timothy:				
Pounds per acre	3	6	12	18
Percentage establishment	18	15	10	8
Perennial ryegrass:				
Pounds per acre	5½	11	22	33
Percentage establishment	65	50	36	25

The effect of increased competition between seedlings was thus to reduce the percentage establishment at the highest seeding rate to less than half that at the lowest rate; that is, increasing the number of seeds sown six times only increased the number of plants which became established by less than three times.

The total number of plants established is not normally critical in determining yield, except in a very short ley to be harvested within a few months of sowing. Thus, to quote an extreme case, Lazenby and Rogers† found that a perennial ryegrass plot with about 400 plants per square metre gave no higher yield than one with about 40. One kilogram of ryegrass seed evenly spread over a hectare would give seeds spaced about 13 cm apart, or assuming a 50% establishment, one plant every 18 cm. Vigorously growing plants quickly produce clumps of 18 cm diameter, so that a continuous cover from

* Davies, W. 'The factor of competition between one species and another in seeds mixtures', *Welsh Plant Breeding Station Bulletin,* Series H, No. 8, 1928.

† Lazenby, A. and Rogers, H. H. *Journal of the British Grassland Society*, **16**, 1961, pp. 153-5

a seed-rate of 1 kg/ha is theoretically possible. Seed-rates as low as this are never used, but rates as low as 5 kg/ha have been found satisfactory in some areas, while in others up to 30 or even 36 kg/ha is commonly sown. An increased seed-rate reduces the time during which bare ground is present, and therefore reduces the chance of weeds establishing; this appears to be the main factor in deciding what seed-rate is necessary. In general, the lower seed-rates are more satisfactory in the drier areas, while the higher rates are normally used in the wetter regions where rapid weed establishment is a more serious problem.

If more than one species is included in the seeds mixture, competition between the different species must also be taken into account. In the establishment of leys, it is the competitive ability, or *aggressiveness,* in the young plant stage which is important. This may be markedly different from the aggressiveness of the mature plant; thus, for example, creeping bent has a small seedling and does not compete strongly in the early stages of growth, but the mature plant, with its strongly-creeping habit, can be highly aggressive and spread at the expense of other species.

Of the grasses commonly sown in leys, Italian ryegrass is the most aggressive in the early stages, closely followed by perennial ryegrass. Cocksfoot, timothy and meadow fescue are much weaker competitors at this stage; the following figures* illustrate the effect on the percentage establishment of timothy of varying quantities of other species: 1 lb/acre = 1·12 kg/ha)

Mixture (per acre)	6 lb timothy + 5 lb PRG	6T + 11PRG	6T + 33PRG
% establishment of timothy	22	13	7
Mixture	6 lb timothy + 5 lb cocksfoot	6T + 11C	6T + 33C
% establishment of timothy	22	17	14
Mixture	6 lb timothy + 10 lb MF	6T + 20MF	6T + 40MF
% establishment of timothy	17	22	21

PRG = Perennial ryegrass
MF = Meadow fescue

The establishment of timothy is thus markedly reduced by the competition of perennial ryegrass unless the latter species is present in very small quantity (it should be remembered that 33 lb ryegrass contains less than one-and-a-half times the number of seeds present in 6 lb timothy). The competition from cocksfoot is much less severe,

* Davies, W. *op. cit.*

and that from meadow fescue negligible. Thus a mixed timothy-meadow fescue sward (with cocksfoot also, if required) is comparatively easily produced, whereas mixtures of perennial ryegrass (or still more, Italian ryegrass) with the other species normally give a sward dominated by ryegrass, unless the management is such as to hold the ryegrass severely in check.

Competition between different cultivars of the same species is not so readily observed as that between different species. In general the more upright earlier-flowering cultivars tend to be slightly more competitive in the young plant stage than more prostrate later-flowering ones. The difference however is not usually great, and it may be said that different cultivars are not mutually exclusive, and that their reactions to different types of management show less difference than that between those of different species. It is therefore possible to establish and maintain, at least for some time, swards containing two or more cultivars of the same species; thus, by using cultivars of different growth rhythm, the production of a simple mixture can be extended or levelled out, without the attendant management difficulties consequent on including other species. It is therefore a common and often desirable practice to include for example an early and a late perennial ryegrass, or a medium large and a wild-white clover, both in simple and in general-purpose mixtures.

Taking these various factors affecting establishment and competitive ability of the different species and cultivars into account, it is possible to design an almost infinite number of different seeds mixtures. These however fall into a relatively small number of groups. The short leys are essentially based on ryegrasses, and range from the rarely used ultra-short ley, of less than twelve months duration, based on Westerwolds ryegrass, through the one-year leys, usually of Italian ryegrass alone, to the two- or two-to-three-year leys where Italian is supplemented by the longer-lived hybrid and perennial ryegrasses. For these short leys no other grass species is sufficiently rapid-growing and high-yielding, but within each type of ryegrass a number of different cultivars may be used. Such short leys are usually intensively managed with high nitrogen inputs, but red clover may on occasion be included.

Seeds mixtures for leys of three years duration or longer can contain a single species or a mixture of two or more; here again each species may be represented by one or more cultivars. Perennial ryegrass, as the highest-yielding and most easily established species, is by far the most commonly used grass, both on its own and in mixtures. Cocksfoot, timothy and meadow fescue give, under most conditions, lower yields of digestible dry matter, but are of value

under conditions and at times of year not favourable to good growth of perennial ryegrass. None is very commonly sown alone, but cocksfoot and timothy are frequently included in mixtures with perennial ryegrass. Mixed ryegrass/meadow fescue swards are rarely practicable, since the latter is so readily suppressed by ryegrass; meadow fescue is therefore used in mixture only with timothy, or with timothy and cocksfoot.

As mentioned above (p. 210), white clover is commonly included in all seeds mixtures for leys of three years duration or longer. It does not compete in such a way as to reduce the establishment of grasses, and indeed, where nitrogen input is low, contributes to their growth. Traditionally, red clover has been included in many general-purpose seeds mixtures, primarily to improve a hay cut taken in the first year of the ley. If sown in sufficient quantity to make a marked contribution to the hay crop it does however compete strongly with the grasses, and the tendency therefore is to confine red clover to special short duration hay leys.

Table 3 gives an indication of the comparative importance of the different types of seeds mixture in British agriculture. The figures are for the areas of sward derived from the various mixtures expressed as percentages of the whole 'sown grass' area of about 2·5 million hectares. They represent an estimate of the position as it was in 1959, but the rate of change appears to be slow, and it is unlikely that more recent figures would show any very marked difference. They bring out both the over-riding importance of the ryegrasses in British grassland farming, and the extent to which multi-species and general-purpose mixtures have been favoured.

Table 3. Swards derived from different types of seeds mixtures as percentage of total sown grass area.

SHORT LEYS				10
Italian alone and Italian + perennial ryegrass	10			
LONGER LEYS & SOWN PERMANENT GRASS				90
Perennial ryegrass alone	16			
Perennial ryegrass + timothy	11			
Perennial ryegrass + timothy + cocksfoot	56			
(*Total ryegrass-based mixtures*		*93*)		
Timothy or meadow fescue or cocksfoot alone	2			
Timothy + meadow fescue	4			
Timothy + meadow fescue + cocksfoot	1			
(*Total non-ryegrass-based mixtures*		*7*)		
Total single grass species mixtures			18	
Total two or more grass species mixtures			72	

Seeds mixture descriptions are based on grass species only and take no account of any clovers included. Data from Idle, A.A. *Journal of the British Grassland Society,* **30**, 1975, pp. 111–20.

Effect of conditions on resultant sward. The composition of the sward which results from the sowing of a multi-species seeds mixture is very much affected by climatic and soil conditions. Figures taken from reports by Greenaway and Budden* illustrate these effects. Two contrasting standard general-purpose mixtures were sown in a number of fields in different areas, and the resulting swards later analysed. The figures given are for the amounts of the individual sown grass species, expressed as percentages of the total sown grass cover; clovers are ignored, since the amount of clover is so much a function of the exact age of the sward and of the method of management. For the sake of simplicity unsown grasses and weeds are also ignored, and average figures for several fields are used, since this will tend to even out any differences in the standard of management practised by the different farmers. Fields in dry areas (those with an irrigation need in eight or more years out of ten) are compared with those in wet areas (irrigation need in less than five or six years out of ten), and those with free-draining soil compared with those showing impeded drainage.

One mixture was of the very popular type known, from the name of the station where the trials on which it was based were carried out early in this century, as a Cockle Park mixture. It consisted of 11 lb perennial ryegrass, 8 lb cocksfoot, 4 lb timothy, 3 lb red clover and 1 lb white clover per acre (1 lb/acre = 1·12 kg/ha). The figures quoted for sward composition are for the second year after sowing. It happened that the only fields showing markedly impeded drainage were

	Perennial ryegrass	Timothy	Cocksfoot
Percentage by weight of seeds in mixture	48	17	35
Percentage by number of seeds in mixture	26	38	36
Percentage in sward, free-draining fields			
Dry areas, irrigation need 8–10 years	52	14	34
Wet areas, irrigation need 0–6 years	58	22	20
Percentage in sward, impeded drainage			
Intermediate areas, irrigation need 6–8 years	54	30	16

* Greenaway, T. E. and Budden, M. 'A discussion on the influence of relative moisture availability on the swards resulting from standard seeds mixtures. I. Mixtures of the Cockle Park type. II. Swards produced from a cocksfoot/timothy/meadow-fescue mixture', *Journal of the British Grassland Society*, **13**, 1958, pp. 222–8; **14**, 1959, pp. 117–23.

in areas with intermediate irrigation need, and figures for these are included for comparison.

A similar trial with a non-ryegrass general purpose mixture consisting of 8 lb meadow fescue, 4 lb timothy, 6 lb cocksfoot and 2 lb white clover per acre included fields with impeded drainage in dry and wet areas. Here the figures, which are averages of the first two years, were as follows:

	Meadow fescue	Timothy	Cocksfoot
Percentage by weight of seeds in mixture	45	22	33
Percentage by number of seeds in mixture	22	45	33
Percentage in sward, free-draining fields			
Dry areas, irrigation need 8–10 years	39	18	43
Wet areas, irrigation need 0–5 years	48	25	27
Percentage in sward, impeded drainage fields			
Dry areas	32	36	32
Wet areas	42	36	21

These survey results indicate that general purpose mixtures can produce swards of reasonable composition under a wide range of climate and soil conditions, but that these conditions do have a marked effect. It will be observed that timothy and cocksfoot are very much affected by the available water; they tend to vary inversely, so that the inclusion of both in the same mixture might be considered somewhat illogical. It can be argued however that while average expected rainfall and soil characteristics may be known, weather cannot be predicted, and the use of such mixed-species swards is a reasonable safety measure, ensuring fairly satisfactory results under almost any conditions.

The figures also illustrate the different competitive abilities of the different species, and the frequent wide divergences between proportions of a species in the mixture sown and in the resultant sward.

MANAGEMENT OF GRASSLAND

The primary object of the management of grassland is the production of the maximum possible food for animals. It is necessary, therefore, to consider the methods of management and utilization which will

give this maximum yield of food; and, in addition, since grass is a crop that is expected to continue to yield throughout the season, and in many cases for several or even many years, to consider the effects of such management on the plants themselves, and hence on their future yield.

Yield in grasses, and the ways in which it is influenced by different methods of utilization have been discussed (p. 133), and the position need only be summarized here. Although grasses are tolerant of frequent cutting or grazing, they, like other green plants, depend on their leaves for photosynthesis. Cutting or grazing will reduce the area of leaf, and hence the amount of photosynthesis, and consequently the yield. The maximum total yield of dry matter is therefore obtained by the most lenient cutting or grazing. On the other hand, the longer the grass is allowed to grow, the lower will be the quality of the produce, since protein content is at a maximum and fibre content at a minimum in the youngest grass. The art of management for the production of maximum useful food lies largely in balancing these two opposing tendencies. In general, the higher yields are obtained by on-and-off (*rotational*) grazing in which growth is allowed to proceed unchecked for several weeks, and the produce then grazed off, followed by a further rest-period, and so on. Continuous grazing for long periods, if it is sufficiently hard to keep the grass always short, will result in low total yields, although the yield which is produced will be of high nutritional value. Lighter continuous stocking may give higher yields, but is normally less satisfactory. It necessarily involves the use of a comparatively large area per head of stock, and there is then a considerable danger of unequal and selective grazing, with overgrazed patches giving low yields, and undergrazed parts being allowed to grow so long that they become unpalatable.

In a short ley, high yield will normally be almost the only consideration, and the grazing and the conservation cuts will be arranged accordingly. In a longer ley it is however necessary to consider not only the immediate yield, but also the effect of treatment on the future behaviour of the sward. The frequency of defoliation will affect not only the yield; it will also affect the root system and other non-photosynthetic parts of the plant. A plant which has been grazed hard will have a smaller root system and smaller reserves than one which has been allowed to retain a larger leaf area. This is illustrated by the following figures* for weight of roots and plant bases in a block of turf 4 in in diameter and 6 in deep (10 × 15 cm) taken from swards which had previously received different treatments:

* Jones, M. 'Grassland management and its influence on the sward', *Empire Journal of Experimental Agriculture,* I, 1933.

Sward	Lightly grazed (g)	Hard grazed (g)
Three-year mixed ley	29	19
Old pasture	58	40
Perennial ryegrass only	33	27
Cocksfoot only	41	19

It will be seen that in all cases the weights were lower in the samples from areas which had previously been hard grazed. The higher weight in the old pasture samples shows the tendency towards the formation of a 'mat', a dense accumulation of roots and plant bases which may be deleterious if it proceeds too far, but even here the difference is still apparent. It will also be seen that different grasses are differently affected; perennial ryegrass is comparatively little reduced by hard grazing, whereas cocksfoot shows a very marked difference. This is due largely to its ability to store food reserves in its succulent white leaf-sheath bases if photosynthesis is allowed to proceed. A grass plant with large root system and food reserves is naturally able to make stronger growth, and to compete more strongly with other species, than one in which these are reduced. Cocksfoot is thus favoured by lenient grazing or long rest periods, and may become dominant in undergrazed swards on soils of fairly high fertility. Perennial ryegrass is very tolerant of hard grazing, and is favoured, compared with cocksfoot (and to a lesser extent with timothy and meadow fescue) by the resulting absence of shading.

Not only do different species react differently to varying intensities of grazing, they are also differently affected by the actual time of grazing. Different species grow at different times during the season; hard grazing during the growing period will cause a check because young leaves are eaten off as fast as they grow, while grazing during a dormant period will have comparatively little effect. Perennial ryegrass (particularly the early types) is amongst the first grasses to commence growth in spring, followed by cocksfoot (this may be earlier if it has large reserves resulting from autumn resting) and then usually by meadow fescue and timothy. White clover is also late in starting spring growth, as are bent and Yorkshire fog. The proportion of the different species in a sward can be greatly altered by the timing of the grazing. Thus Martin Jones found in his classic work at Jealott's Hill Research Station that a young ley grazed hard throughout the spring (and rotationally grazed during the rest of the year) for three successive years, had a final composition of 41% ryegrass, 16% cocksfoot and 34% clover. Another part of the same ley, treated in exactly the same way except that hard grazing was

confined to early spring, showed only 11% ryegrass and 4% clover, but 82% cocksfoot. In the first case both grasses were kept in check until late spring, allowing strong growth of the clover, but not seriously harming the ryegrass. In the second case the hard grazing stopped at the time cocksfoot was beginning to grow, and the ensuing rest-period strongly favoured this species and enabled it to become dominant and to shade out much of the ryegrass and white clover.

He obtained even more striking results on old pasture by varying the intensity of stocking only, all other conditions being kept the same.

This old pasture was initially of low value, with 10% of good grasses and 10% of clover, the remainder being weed grasses. One section was very well grazed, the number of sheep being carefully adjusted to suit the amount of keep available, so that both overgrazing and undergrazing were avoided. The composition of the sward at the end of two years was 33% useful grasses (mainly ryegrass), 54% white clover and 13% weed grasses. On another section of the same sward a constant number of sheep were grazed throughout the whole time, so that there was excessive overgrazing in winter and early spring and very marked understocking in summer. The composition of this section at the end of the two years was 7% useful grasses, 3% clover and 89% weed grasses, mainly bent and Yorkshire fog; that is, it was even poorer than at the start of the trial. While the large differences obtained in this trial were the result of very carefully managed grazing on the one hand, and of intentionally very bad management on the other, the same tendencies operate under normal farm conditions. There is almost always greater pressure on the available keep when this is short in spring, and difficulty in keeping abundant growth in summer adequately grazed. The tendency towards overgrazing at one period, and undergrazing at the other, is thus difficult to avoid, and is one of the main causes of the deterioration of grassland swards.

The maintenance of a balance between grasses and legumes is, as the trials quoted illustrate, largely a matter of grazing management. Providing adequate lime and phosphate (and to a lesser extent, potash) are available, the white clover content of a sward can be readily increased by hard grazing, particularly in late spring. Conversely, an excessively clovery sward can be improved by favouring the growth of grasses by increasing the length of rest-period. Nitrogenous manuring will also favour the grasses; heavy nitrogen dressings plus long rest-periods will give high yields, but will result in an almost pure grass sward.

The two alternative sources of nitrogen are only additive to a small extent. The yield of the better grasses is very roughly proportional to

the available nitrogen up to perhaps 400 kg/ha of nitrogen per annum, with in some cases further but lower rates of yield increase up to perhaps 600 kg/ha of nitrogen. The yield from a good clovery sward, without added nitrogen, may, according to conditions, be equivalent to that from an all-grass sward with some 150–200 kg/ha of nitrogen applied as fertilizer. Addition of a small amount of fertilizer nitrogen to such a clovery sward cannot be relied on to increase yields; it may well merely result in a decrease in clover and a consequent reduction in clover nitrogen supply. Under such conditions the yield may remain approximately constant with an increasing fertilizer nitrogen input until the 150–200 kg/ha level is reached, and thereafter the response is that of an all-grass sward. In practice, the clover present is rarely fully efficient, so that usually some yield increase is obtained from small applications of nitrogen. Nevertheless, it is necessary to make a choice, and aim for moderate yields at relatively low cost from a clovery sward, or for maximum yields from an all-grass sward with high fertilizer nitrogen input.

Neither choice will be satisfactory under drought conditions; both white clover growth and response of grasses to applied nitrogen are very much reduced if there is a marked water deficit. Consistent maximum yields can thus usually only be obtained where irrigation is practicable.

Cutting of grass for silage or dried grass has approximately the same effect as grazing if the period of growth is the same, except that the treading action of stock, which may be beneficial in causing increased rooting from nodes near ground-level, is absent, and that there is no return of manurial ingredients in dung and urine. The period between cuts is often long, and if this is so, shading effects come in. These are still more important in the case of cutting for hay, which markedly favours the taller-growing plants and those capable of benefiting, by storage of food reserves, from an unusually long period of undisturbed growth. Cocksfoot and timothy, for example, are both favoured by haying in comparison with the higher light-demanding perennial ryegrass and white clover. Red clover is also favoured at the expense of white clover. The effects of haying are most marked if the field is laid up for a long period and the hay cut at a late stage. If this stage is so late that some of the plants present are able to produce ripe seeds an opportunity is offered for very marked change of sward type by self-seeding. Such a change is, under British conditions, almost always a change for the worse, since the early-ripening seeds are mainly those of weedy annuals or short-lived perennials. Among grasses, the most important of these are soft brome and Yorkshire fog, the former in particular being a charac-

teristic weed of over-hayed grassland. Among non-gramineous plants, yellow rattle and hog-weed are also characteristic of such swards.

The higher-yielding herbage plants all require a high level of soil fertility, and cannot be grown satisfactorily unless this is maintained. Establishment of the sown species is poor under conditions of low fertility, and complete manuring is usually desirable when sowing down to grass. This should include nitrogen, since at this stage combined nitrogen from legumes is not yet available. None of the high-yielding herbage plants will tolerate high acidity or continuous waterlogging, and liming and drainage may therefore also be necessary.

In an established grazing ley under good conditions there is a constant and rapid circulation of nutrient elements; nitrogen, phosphorus, potassium and calcium are absorbed from the soil by the grazing plants; these are grazed by the stock and the dung and urine of the grazing animal returned to the soil, where it rapidly decomposes and its elements are again taken up by the plants. The circulation is, however, incomplete; only part of the nutrient elements is returned to the sward, the remainder, varying in proportion with the class and age of stock, goes to provide milk or meat. Losses by leaching from the soil also occur, and although an ample nitrogen supply may be maintained if clover is abundant, the available supply of other elements will be gradually reduced if additional fertilizers are not supplied. The first effect of this reduction in fertility will be that the yield of the plants present will fall off; as their yield falls so their competitive ability falls also, and other plants, better adapted to the lower fertility conditions now prevailing, will tend to replace them. Under these conditions decay of dead plant residues tends to be slower, with a resultant increase of mat formation, so that further manurial elements remain locked up and unavailable. If available lime and phosphorus are so reduced that the clovers become less abundant, the nitrogen supply will also be reduced, and a further lowering of the level of fertility will result.

The ryegrasses are the plants least adapted to low fertility, and reduction in the proportion of ryegrass in the sward is usually one of the first effects of such a lowering of fertility. Cocksfoot, timothy and meadow fescue are somewhat more tolerant, but still need at least a moderately high level; at lower fertility levels, bent, with its vigorously competitive creeping habit, Yorkshire fog, and perhaps crested dog's-tail, sweet vernal, and the small fescues as well as many non-gramineous weeds, will come in. The change from a sward dominated

by perennial ryegrass to one in which bent is dominant is perhaps the commonest of all forms of deterioration of leys. Bent is favoured not only by a reduction in fertility, but also, as has been seen, by the natural tendency towards overstocking in spring and understocking in summer. Invasion by bent so commonly accompanies the ageing of leys, and is so commonly the main reason why they are eventually broken up, that it is often regarded as an almost inevitable stage; certainly the preservation of a productive ryegrass sward, free from bent, is a good test of grassland management.

The change of sward-composition with change of fertility level is a reversible one, and adequate manuring of a sward composed of low-yielding, low fertility-demanding plants can result in a very marked improvement. Even an extremely low-yielding mountain sward, dominated by molinia and nardus, can be changed, by heavy manuring and liming only, to a reasonably good white clover-grass sward of lowland type, the seeds of the new species being brought in by wind and stock. Lowland swards of low fertility often respond well to lime and phosphorus only, the increased white clover content resulting from the addition of these elements having the effect of increasing the nitrogen supply, and this in turn favouring the growth of better grasses. Bent, however, once established, is not easy to eradicate by manuring and management alone, and it may often be more profitable to destroy the existing vegetation by ploughing, or the use of paraquat, and to start again with a new ley, with a higher fertility level produced by manuring. Direct drilling into paraquat-killed turf may sometimes be possible.

Where it is undesirable to plough, improvement may be assisted by grassland cultivations. Severe harrowing and surface cultivation may tear out some of the surface-creeping species such as bent; they also, by increasing aeration, assist in the breakdown of mat and therefore in the setting free of locked-up fertility. Without adequate manuring, however, such cultivations can rarely be expected to produce very marked results. Alternatively, it may be possible to make selective use of herbicides for at least partial control of undesirable grass species. Paraquat and dalapon, at high rates of application, kill most grasses, but at low rates are selective in their effects. The effects are not always easy to predict precisely, but, for example, perennial ryegrass is generally resistant to dalapon at about 3 kg acid equivalent per hectare (some difference between cultivars has been reported), while many of the less desirable grasses, such as bents, sweet vernal and Yorkshire fog are susceptible.

Oversowing with desirable and readily establishing species such as perennial ryegrass and white clover may be satisfactory where the existing sward is thin and open.

EVALUATION OF GRASSLAND

Botanical analysis. Since different grassland species vary in their yield and nutritive value, the botanical composition of a sward gives a measure of its agricultural value. For many purposes simple inspection and a visual estimate of the approximate abundance of different species is sufficient. Where, however, it is desired to compare different swards, as, for instance, in trials of the effect of different treatments, it is necessary to use some more precise numerical measure of the proportions of different species present. The figure assessed may be proportion by number, proportion of ground area covered, or proportion of total weight of herbage.

Proportion by number. It is rarely possible to determine the extent of individual plants, particularly of creeping species, in dense herbage. The unit used is therefore the individual tiller, and the method is sometimes known as the *percentage tiller frequency* method. A grid of convenient size (say 15 × 15 cm) is thrown repeatedly at random within the area to be assessed, and the number of tillers of each species standing within the grid area reckoned. Figures from repeated throws are totalled and the average figure for each species expressed as a percentage. For very accurate work actual counts are made (with very short herbage it may be necessary to lift the square of turf enclosed by the grid); but often sufficiently close estimates of numbers can be made without actual counting. The main disadvantage of the method is that it cannot be strictly applied to non-gramineous herbage; various arbitrary conventions have to be adopted to deal with white clovers and weeds.

Proportion of ground area covered. If the proportion of the area of each quadrat (the individual area sampled, i.e. the space enclosed by the grid at one throw) covered by the different species is recorded instead of tiller numbers, an average number for *percentage area* can be obtained. This method has the advantage that it can be readily applied to all types of herbage plants, including clovers and rosette plants, and also used to give the proportion of bare ground, which is necessarily ignored in the counting method. Its main disadvantage is that it depends on eye estimation; it can be made more accurate by subdividing the grid into small squares, but is never strictly objective.

A useful modification of the area method is the *point quadrat* method, which may be regarded as the use of a very large number of quadrats, each reduced to negligible size. A horizontal frame carries ten movable wires, each of which can be brought down vertically or

diagonally until the point touches vegetation or bare ground. The number of times a given species is touched in, say, 200 'points' can be regarded as proportional to the percentage area occupied by that species. Since the method avoids estimation, and involves only recognition of the species touched, it is readily reproducible, and closely comparable results can be obtained by different observers. It is, however, not readily applied to tall herbage.

The inclined point quadrat, using a single point the position of which can be accurately recorded, is used for detailed studies of the sward canopy.

Proportion of total weight of herbage. Herbage can be clipped at a standard height (usually as near ground-level as possible) from a number of quadrats, and the cut herbage sorted out into the constituent species, which are then weighed. This technique, known as the *percentage productivity* method, gives a figure for each species which represents the percentage of the whole yield at the time of sampling which is contributed by that species. It is thus a more directly useful method when considering the productivity of a sward, but is necessarily extremely slow and laborious. A similar method, but using estimated proportions of yield instead of actual weights, is quicker, but, like all estimation methods, is reliable only when used by an experienced observer, and results obtained by different observers are not always strictly comparable.

Grassland yield trials. Botanical analysis, by recording the proportions of high- and low-yielding species in the herbage, enables an approximate estimate of the potential yield of a sward to be made. Such an estimate depends, of course, on a previous knowledge of the yielding ability of the different species, and to obtain this knowledge, and to compare actual yields of different swards, yield trials are necessary. Yields may be recorded as total production per hectare over a given period, expressed either as fresh weight, dry weight, or starch and protein equivalent; or, since animal feeding is the object of growing grass, directly as live-weight gain or in terms of milk production.

Herbage yields. Figures for yield of herbage can be readily obtained by direct cutting and weighing, but they will vary very much according to the frequency of cutting. Except where an attempt is being made to estimate production of silage or hay, yield figures so obtained will bear little relation to yield under normal farm conditions. A closer approximation to yield under pasture conditions can be obtained by

the *movable-cage* method, where areas of pasture are temporarily protected from grazing. Cuts are taken from similar areas of protected and of grazed sward, the difference in weight between the two giving an estimate of the weight of herbage grazed off. Various precautions are necessary, but, providing the individual grazing periods are short, the method gives results of considerable value, and it has been widely used.

There are also a number of non-destructive techniques for yield estimation which do not involve cutting and weighing of all samples. In the visual standard core comparison method, a graded series of sward cores of known foliage weights are used. The weights of herbage on a whole series of quadrats similar in size to the cores can then be estimated by matching them visually against the standard cores. In the 'grass-meter' the herbage supports a light metal disk sliding on a vertical column, and the height of the disk above ground level gives a measure of the amount of herbage under it. The method is suitable only for the comparison of grazed swards of closely similar type. In the capacitance probe method, a framework of insulated metal pillars is used. The pillars are electrically connected to form the plates of a condenser, with the air as the dielectric between them. If the framework is placed in standing herbage, the capacitance of the condenser will vary with the amount of herbage now present in the air between the pillars. The instrument can be calibrated by recording the capacitance on a number of areas of sward which are then cut and weighed. Re-calibration is necessary for different types of herbage and different water contents, but providing this is done, the method is capable of giving fairly reliable results without necessitating any cutting of plots other than for the initial calibration. A somewhat similar method involving the recording of the degree of attenuation of beta-rays passing through the herbage has also been proposed.

Animal production. All these methods of yield estimation may be usefully supplemented by *in vitro* determinations of digestibility so that yields can be expressed in terms of digestible organic dry matter. Further determinations of proteins and soluble carbohydrates, and of cell wall and cell contents proportions may also be useful. The majority of the methods, other than the moveable cage technique, are however methods of assessing amounts of herbage on offer to animals, rather than amounts actually consumed. The most complete assessment of the value of a sward is provided by figures for the animal production obtained from it; these can only be obtained by directly recording the animals themselves. Such methods are necessarily laborious and expensive and, while of great value in providing

yield figures directly in terms of animal production, are clearly not suitable for small-plot trials where numerous different swards are being compared.

LAWNS AND SPORTS TURF

Lawns and sports turf may be briefly considered as a type of grass sward very distinct from those of agricultural grassland. The object desired is a dense, low-growing cover of evergreen herbage; yield is of no importance, and high yield is, in fact, a disadvantage as necessitating more frequent mowing. The main requirements in a lawn grass are that it shall tolerate close mowing and shall produce a dense, uniform stand; where the turf is used for games it must not be slippery when wet (ruling out white clover) and must be capable of withstanding hard wear. If used for games where the ball must run true, the individual tillers must be as small as possible.

It is thus the low-growing, low-yielding grass species, mainly of low agricultural value, which are the best lawn grasses. The smaller bents, *Agrostis tenuis* (brown-top), *A. canina* (velvet bent) and selected cultivars of *A. stolonifera* (creeping bent), and forms of *Festuca rubra* (red fescue) are the best for first quality lawns and sports turf. For general lawns and playing-fields, perennial ryegrass (pasture and amenity cultivars only), diploid timothy (Aberyswyth S 50 and amenity cultivars) and sometimes crested dogstail may be used; although less fine-growing they withstand hard wear and puddling in winter better than the finer grasses. Smooth-stalked meadow-grass is sometimes used where drought and wear resistance is important, but it is slow to establish; for very shady conditions wood meadow-grass (*Poa nemoralis*) has been recommended, but does not form a good turf.

Lawns and sports turf are established either by turfing or seeding. Turfing is expensive, but gives a usable sward quickly; turves can usually be readily established during the winter, but must not be allowed to dry out during the critical period before new roots have penetrated into the underlying soil. The composition of the sward produced will, of course, intially be that of the sward from which the turves were cut, but the changed conditions resulting from transplanting to a new environment may result in considerable alterations of composition. Thus, for example, Cumberland sea-washed turf, extensively used for the production of bowling greens, consists mainly of specialized ecotypes of red fescue, selected by the particular conditions of the salt-marsh environment; when this is transplanted to a different soil under very different environmental conditions very marked changes of composition may take place.

For the establishment of lawns from seed, very high seed-rates are usually employed in order to give quick cover and to prevent as far as possible the establishment of weeds. Rates of 2 oz per square yard (say 60 g/m², equivalent to 600 kg/ha) have often been recommended, but for most purposes there is little advantage in exceeding $\frac{2}{3}$ oz (say 20 g/m²), while for grass paths and similar areas $\frac{1}{3}$ oz (10 g/m²) is usually satisfactory if very quick cover is not essential. Very high purity of seed is desirable, as a small proportion of weed grasses, too low to be of any significance in agricultural practice, may result in considerable disfigurement of a lawn; the effect is, of course, much enhanced by high seed-rates. A typical seeds mixture for fine lawns, golf and bowling greens consists of 70 to 90% by weight of red fescue (1·5 million seeds per kg) and 10 to 30% of brown-top (12 million per kg). The red fescue normally recommended is the non-creeping subspecies Chewing's fescue, since a mixture of two creeping grasses may result in patchiness. Creeping red fescue may be sown alone. Red fescue, although tolerant of acidity, low fertility and drought, does not however stand up well to hard wear, and most hard-used bowling and golf greens are reported* to consist largely of brown-top and annual meadow-grass. It is suggested therefore that brown-top alone could be sown.

Similarly, cricket squares, traditionally sown with a mixture of 60% Chewing's fescue, 20% brown-top and 20% crested dogstail, were found to consist mainly of brown-top and annual meadow-grass, with smaller proportions of perennial ryegrass and rough-stalked meadow-grass and only occasional red fescue. Here it is suggested that brown-top sown alone, with an oversowing of perennial ryegrass into the established bent (to avoid excessive seedling competition) would be adequate. On football pitches the amount of wear may be too great even for brown-top, and the main constituents of heavily used pitches are perennial ryegrass and annual meadow-grass. Perennial ryegrass alone, reseeded each spring if necessary, might therefore be used; time does not usually permit satisfactory establishment of the potentially useful smooth-stalked meadow-grass.

Management of lawns and sports turf differs markedly from that of agricultural grassland. Frequent mowing is normally essential, but, since constant close mowing has a weakening effect on all grasses, by keeping the leaf area very small, mowing height should be varied when conditions permit, to allow of some reserves being built up. Nitrogenous manuring is necessary; sulphate of ammonia is normally used, and the acidifying effect of repeated dressings encourages the

* Adams, W. A. 'Some developments in the selection and maintenance of turf grasses', *Scientific Horticulture,* **26**, 1975, pp. 22–7.

acid-tolerant bents and fescues and discourages clovers. Ferrous sulphate is also used with this object. Phosphate and potash are needed in amounts depending on whether or not mowings are removed; liming and excess phosphate will tend to give a clovery turf. Constant machine-mowing, even without extra rolling, tends to produce an over-consolidated soil surface, and raking, aerating by means of hollow-tine forks or spiked rollers, and top dressings of screened humus. etc., are necessary to maintain satisfactory growth. Since clovers are not required, selective weed-killers may be freely used for the destruction of dicotyledonous weeds.

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Official notices relating to the National Lists of cultivars, and to additions to and deletions from these are published in the *Plant Varieties & Seeds Gazette.*

LEAFLETS

Leaflets dealing with most of the major agricultural and horticultural crops are published by the Ministry of Agriculture, Fisheries and Food.

The National Institute of Agricultural Botany publishes classified lists of varieties of cereal and herbage crops which supplement the information in the *Plant Varieties & Seeds Gazette* by giving a brief indication of performance. The N.I.A.B. also issue a series of *Farmers Leaflets* and *Vegetable Growers Leaflets* covering most major crops. These leaflets, which are revised annually, give more detailed information on the better cultivars, and in many cases include Recommended Lists; they provide the best source of up-to-date information on cultivars. These and other publications are supplied free to Fellows of the N.I.A.B.; details of the Fellowship Scheme, and the special scheme for students, may be obtained from The Secretary, N.I.A.B., Huntingdon Road, Cambridge.

GLOSSARY

Achene: a small, dry, one-seeded indehiscent fruit.
Actinomorphic: symmetrical about more than one diameter; regular.
Adnate: united with another part of a different kind.
Adventitious: out of the ordinary course; applied, for example, to roots arising from a stem or buds arising from a root.
Allopolyploid: polyploid derived from more than one species.
Amenity cultivar: cultivar not intended for use as a productive crop; e.g. a lawn grass.
Amphidiploid: allopolyploid containing diploid complements of both parent species.
Amylase: enzyme catalysing breakdown of starch; includes α-amylase which attacks glucose linkages at any point in molecule.
Amylopectin: constituent of starch, with branched chains of glucose.
Amylose: constituent of starch, with unbranched chains of glucose molecules.
Anatropous ovule: inverted so that the funicle and micropyle are adjacent.
Androecium: the stamens considered as a whole; the male part of the flower.
Aneuploid: irregular chromosome number due to loss or gain of single chromosomes, not whole sets.
Annual: completing its life cycle within a year.
Anterior: facing outwards away from the axis, usually towards the bract.
Anther: the part of a stamen which contains pollen.
Apetalous: without petals.
Apical: at the apex.
Apocarpous ovary: with the carpels free from one another.
Apomictic: producing seed without fertilization.
Appressed: pressed flat and close to an organ.
Ascending: curving upwards.
Assimilates: products of photosynthesis.
auct.: of authors, i.e. has been used but is not valid name.
Autogamous: self-pollinating.
Awn: bristle-like structure on lemma, etc.
Axil of leaf: the angle between the leaf and stem.
Axillary: arising in the axil of a leaf or bract.

Beak of a fruit: a narrow prolongation.
Berry: a fleshy fruit without a hard layer of pericarp around the seeds, usually with several seeds.
Biennial: completing its life within two years and flowering in the second year only.
Bifid: deeply divided in two.
Blade of a leaf: the flat part or lamina.
Bract: a leafy structure beneath a flower or group of flowers.
Bracteole: a secondary bract, as on the pedicel of a flower.
Bulb: a swollen underground bud with fleshy scales and/or leaf bases on a short stem.

c.: abbreviation of *circa*, about.
Calyx: the sepals considered as a whole.
Cambium: a layer of cells dividing to produce phloem externally and xylem internally. See also *cork cambium.*

Canopy: leaf cover.
Capitate: having a rounded head.
Capsule: a dry dehiscent fruit derived from two or more united carpels.
Carpel: one of the units composing the gynaecium (or pistil) and containing one or more ovules.
Caruncle: a warty or fleshy outgrowth from the surface of a seed, near the micropyle.
Cauline leaves: borne on an aerial stem.
Caryopsis: a dry one-seeded fruit with the pericarp and testa fused together.
Cell: basic unit of plant structure.
Cellulose: complex carbohydrate with long unbranched chains of glucose isomer; constituent of plant cell walls.
Central fusion nucleus: diploid nucleus formed by fusion of two haploid nuclei of embryo-sac, and fusing with male nucleus to give triploid endosperm nucleus.
Chlorenchyma: tissue containing chlorophyll.
Chlorophyll: the green pigment of plants, concerned with photosynthesis.
Chromosome: thread-like structure in nucleus carrying genetic information.
Ciliate: (i) having cilia or flagella, (ii) having a marginal fringe of long hairs.
Cleistogamous flowers: not opening, pollination taking place within the closed flower.
Coleoptile: bladeless first leaf of grass seedling.
Collenchyma: tissue consisting of cells with walls strengthened by layers of cellulose, with the thickening mainly at the corners.
Commercial variety: cultivar produced by repeated seeding without special selection of mother seed.
Common catalogue: combined national lists of E.E.C. countries.
Compound leaves: composed of two or more separate leaflets.
Connate: united with another part of the same kind.
convar.: abbreviation of convarietas.
Convarietas: taxon smaller than a subspecies, but including several groups, each referred to as a varietas.
Cork cambium: a layer of cells which divides to produce cork cells.
Corm: a rounded, swollen, fleshy underground stem, outwardly resembling a bulb, but solid.
Corolla: the petals considered as a whole.
Corpus: central part of apical meristem.
Cortex: the tissue between the epidermis (or the piliferous layer of roots) and the endodermis or starch sheath.
Cotyledon(s): the first leaf (leaves) of a seed forming part of the embryo.
Culm: the aerial stem of a grass or sedge.
Cultivar: cultivated variety, named variety in agricultural or horicultural sense; term used in scientific literature to avoid possibility of confusion with botanical variety or varietas.
Cuneate: triangular and attached at the point; of leaf bases.
Cuticle: impervious layer on surface of epidermis.
Cutin: wax-like substance, main constituent of cuticle.
cv.: abbreviation for cultivar.
Cyme: inflorescence in which each axis terminates in a flower, with growth continued by side branches.
Cymose: in the form of a cyme.
Cytoplasm: the protoplasm other than the nucleus.

DDM: digestible dry matter.
Deciduous: falling off, usually when mature.
Decumbent: lying on the ground but ascending at the end.
Decurrent leaf: having the base prolonged down the stem often in the form of wings or projections.
Decussate leaves: in pairs, opposite, each pair at right angles to the succeeding pair.
Dehiscent: opening to shed seeds (or spores).
Diam: an abbreviation of diameter.
Diarch: having two strands of xylem.
Diaspore: structure by which plant is

propagated, whatever its morphological nature; used here mainly in sense of 'agricultural seed'.

Dioecious: having male and female flowers on different plants.

Diploid: with two sets of chromosomes.

Dissected: deeply cut into narrow lobes.

Distichous: in two opposite vertical ranks.

DM: dry matter.

DODM: digestible dry organic matter, i.e. DDM less ash.

Drupe: a fruit with the outer part fleshy and the seed enclosed in a woody layer of pericarp.

D-value: DODM expressed as percentage of DM.

Ear: general term for cereal inflorescence.

Emarginate: with a shallow notch at the apex.

Empty glume: obsolete term for glume.

Endodermis: a single layer of cells between the cortex and the vascular tissue.

Endosperm: food-storing tissue formed after fertilization outside the embryo of a seed.

Ephemeral: short-lived.

Epicalyx: a whorl of sepal-like lobes close to the clayx.

Epicotyl: seedling stem above cotyledon node.

Epidermis: the outer layer of cells.

Epigeal: above ground; in epigeal germination the cotyledons appear above the soil.

Epipetalous: attached to the petals.

Exstipulate: without stipules.

Extravaginal: outside the sheath.

Extrorse anthers: opening towards the outside of the flower.

f.: abbreviation for forma.

F.1: first filial generation; of cultivars, produced by controlled crossing of two inbred lines and hence uniform and showing hybrid vigour.

Family: group of related genera, smaller than an order, larger than a subfamily or tribe.

Fertilization: fusion of nuclei in embryo-sac.

Fibre: elongated sclerenchyma cell.

Filament: the stalk of a stamen.

Flexuous: wavy.

Floret: (a) small flower, (b) in *Gramineae*, flower plus lemma and palea.

Flowering glume: obsolete term for lemma.

Foliar spray: spray applied to leaves or growing crop generally.

Follicle: a dry several-seeded fruit formed from one carpel and dehiscing along the inner side.

Forma: taxon smaller than subvarietas.

Fortified: of flour, with added nutrients.

Fructification: a general term for a structure bearing spores or containing seeds.

Fruit: the ripened gynaecium (pistil) containing the seeds. Some so-called fruits include additional parts such as the succulent receptacle in strawberry.

Funicle: the stalk of an ovule.

Gametes: male and female haploid cells which fuse to give diploid zygote.

Gametophyte: generation producing gametes; alternates with sporophyte.

Gamopetalous: having the petals united.

Gamosepalous: having the sepals united.

Genera: plural of genus.

Geniculate: bent abruptly or 'kneed'.

Genome: chromosome set of a particular type.

Genus: group of related species; the first part of the Latin name of a plant is that of the genus.

Gibberellic acid: substance promoting growth in length; originally isolated from the fungus *Gibberella.*

Glabrous: not hairy.

Gland: structure secreting essential oil or other special product.

Glandular: acting as gland, provided with glands.

Glaucous: of a pale bluish-green, often somewhat waxy, appearance.

Glume: bract of spikelet in *Gramineae*, not subtending a flower.

Gynaecium: the female part of a flower including the ovary or ovaries and the style(s) and stigma(s).

Habit: the general form of growth of a plant.
Habitat: the place in which a plant grows, plus the external factors associated with that place which affect the growth of the plant.
Halophyte: a plant which can grow in soil containing appreciable amounts of common salt.
Haplocorm: corm formed from single internode of stem.
Haploid: with single set of chromosomes.
Hemiparasite: obtaining part of its food from a host plant.
Herbaceous: not woody; of plants dying down to ground level in winter.
Hermaphrodite: having both male and female parts.
Heterosis: hybrid vigour.
Heterozygous: with homologous chromosomes carrying different genetic information.
Hexamerous: floral parts in sixes.
Hexaploid: with six sets of chromosomes.
Hexarch: with six xylem groups.
Hilum: of a seed, the scar left by the stalk (funicle).
Hirsute: with rather long, rough hairs.
Hispid: bearing stiff hairs.
Hoary: covered with very short hairs which produce a whitish appearance.
Homoeologous: similar but not identical; of chromosomes, not strictly homologous because belonging to different original genomes.
Homologous: corresponding chromosomes of same genome; homologous chromosomes pair at meiosis.
Homozygous: carrying the same genetic information on the two members of a pair of homologous chromosomes.
hort.: of gardens; used of names employed in horticulture, but not valid.
Hypocotyl: the part of the axis between the root and the cotyledons.
Hypogeal: below ground; in hypogeal germination the cotyledons remain below the ground.

Imbricating: overlapping; like the tiles on a roof.
Improvers: substances added to flour to improve bread-making quality.
Inbred line: largely homozygous line produced by continued selfing.
Indehiscent: not opening to release seeds or spores.
Indigenous: native, not introduced from elsewhere.
Inflorescence: a group of flowers on a common axis.
Infraspecific: below level of species.
Infructescence: inflorescence in fruiting stage.
Integument: outer part of ovule; one- or two-layered, growing around nucellus and developing into testa.
Internode: the part of the stem between two successive nodes.
Interspecific: between species.
Intraspecific: within a species.
Intravaginal: within the sheath.
Introrse anthers: opening towards the centre of the flower.
in vitro: in glass; a test carried out using chemical apparatus.
in vivo: in the living animal.
Involucre: one or more whorls of bracts usually below a compact inflorescence (as in *Compositae*).
Irregular: not symmetrical about more than one diameter (zygomorphic).

LAI: leaf area index.
Lamina: of a leaf; the flat part or blade.
Land race: local population of a crop plant selected only by climatic and agricultural conditions.
Lateral: at the side.
Latex: a milky juice.
Leaf area index: ratio of leaf area to area of ground.
Legume: a dry fruit derived from a single carpel and splitting along both sutures.
Lemma: bract subtending a flower in spikelet of *Gramineae.*

Lignified: bearing deposits of the woody material lignin.
Ligulate: strap-shaped. Also used to indicate possession of a ligule.
Ligule: papery prolongation of leaf-sheath at junction with leaf-blade.
Local variety: cultivar derived from mother seed selected by local and agricultural factors, and multiplied for only a few generations under different conditions.
Loculicidal capsule: dehiscing down the middle of each compartment (loculus), between the partitions.
Loculus: a compartment, as in an ovary.
Lomentum: a dry fruit, usually elongated, which breaks transversely into one-seeded portions.
Lyrate: pinnatifid, but having a large terminal lobe and smaller laterals.

Megasporangium: structure enclosing megaspores; ovule in flowering plant.
Megaspore: spore giving rise to female gametophyte.
Megaspore-mother-cell: diploid cell which undergoes meiosis to produce megaspores.
Megasporophyll: leaf-like structure bearing megasporangia; carpel in flowering plants.
Mericarp: a one-seeded portion of a fruit, produced by the ripe fruit breaking into pieces.
Meristem: region of actively dividing cells.
Meristematic tissue: undifferentiated cells which divide to produce further cells.
Mesophyll: parenchyma of leaf.
Metaphloem: later differentiating primary phloem.
Metaxylem: later differentiating primary xylem.
Metabolism: biochemical processes in plant.
Micro-hair: small two-celled hair on epidermis of some grass leaves.
Micropyle: the minute opening in the testa of an ovule through which the pollen tube enters; often visible in the resulting seed.
Microsporangium: structure enclosing microspores; pollen sac in flowering plants.
Microspore: spore which gives rise to male gametophyte; pollen grain in flowering plants.
Microspore-mother-cell: Diploid cell which undergoes meiosis to produce microspores.
Microsporophyll: leaf-like structure bearing microsporangia; anther in flowering plants.
Millenium: one thousand years.
Monoecious: having separate male and female flowers on the same plant.
Monopodial: formed from a single continuous axis.
Mucronate: provided with a minute point.
Multiple fruit: fruit formed from more than one flower.

National list: list of cultivars accepted in a particular E.E.C. country.
Node: the part of a stem from which a leaf arises.
Nucellus: a mass of cells within an ovule and surrounding the embryo sac.
Nut: a fruit containing a single seed and having a woody pericarp; usually derived from a syncarpous ovary.
Nutlet: a small nut, also used for a small nut-like portion of a schizocarpic fruit (*Labiatae* and *Boraginaceae*).

Ob-: reversed, e.g. obovate = ovate but attached by the narrow end instead of by the broad end.
Obtuse: blunt at the tip.
Open pollinated: of a cultivar, multiplied by normal cross-pollination in field, not F.1 hydrid.
Organ: a particular plant structure.
Organelle: a minute organ present in a cell.
Order: a group of related families.
Orthotropous ovule: upright, with the micropyle and funicle at opposite ends.
Outer palea: obsolete term for lemma.
Ovary: the part of the gynaecium containing the ovules.

Ovoid: shaped like an egg in three dimensions.
Ovule: a structure containing an embryo sac and, after fertilization, developing into a seed.

P: probability.
Paddy: rice as threshed.
Palea: bracteole of *Gramineae.*
Palisade layer: specialized layer of mesophyll with closely packed cells elongated at right angles to leaf surface.
Panicle: compound raceme.
Papillose: covered with papillae (pimple-like projections).
Pappus: a ring of hairs or scales at the top of a fruit. A hairy pappus often assists in wind dispersal of the fruit.
Parenchyma: a tissue consisting of living cells with uniform thin cellulose walls.
Pedicel: a flower stalk.
Peduncle: an inflorescence stalk.
Pelleted: of seed or other diaspore, enclosed in inert shell to aid precision drilling.
Pentamerous flower: having the parts in fives.
Pentaploid: with five sets of chromosomes.
Pentarch: with five xylem groups.
Pentosans: polysaccharides formed from pentose sugars.
Pepo: semi-succulent berry derived from inferior ovary of *Cucurbitaceae.*
Perennial: persisting for more than two years.
Perfect flower: having both male and female parts.
Perianth: the part of a flower external to the stamens, including petals and sepals when both present.
Perianth segment: a separate leaf of the perianth, usually used when petals and sepals cannot be distinguished.
Pericarp: the fruit wall, enclosing the seed(s); derived from the carpel or ovary wall.
Pericycle: a layer of non-conducting-tissue one or more cells thick at the periphery of the vascular tissue.
Periderm: a protective layer on the outside of parts of some plants, consisting chiefly of cork and cork cambium.
Perisperm: a food-storing tissue in some seeds, derived from the nucellus.
Persistent: not shed when mature.
Petaloid: resembling petals, often coloured.
Petals: the inner whorl of the perianth, often brightly coloured.
Petiole: the leaf stalk.
Phloem: tissue containing sieve tubes in which elaborated foods are translocated.
Piliferous layer: epidermis of root, some cells of which are elongated as root-hairs.
Pistil: the female part of the flower (gynaecium).
Pistillate: having female parts only.
Pit: aperture in lignified thickening of a cell wall.
Pith: the tissue (usually parenchyma) central to the vascular tissue.
Placenta: the place within the ovary at which the ovules are attached.
Placentation: the arrangement of the placentae and the ovules.
Plasmodesma: cytoplasmic strand passing through cell wall.
Plumule: the embryo shoot in a seed.
Polygamous: having unisexual and hermaphrodite flowers on the same or on different plants.
Polypetalous: having petals free from one another.
Post-emergence: applied after appearance of crop above ground.
Posterior: of floral parts; facing towards the axis.
Pre-emergence: applied before appearance of seedlings above ground.
Precision drill: drill capable of sowing individual seeds or other diaspores singly at predetermined intervals.
Prickle: a sharply pointed outgrowth of the surface of a plant organ.
Primary tissue: tissue formed by differentiation of existing cells, not as a result of cambial activity.
Probability: statistical measure of likeli-

hood that results obtained on samples are due merely to chance; probability of 0·01 (= 1%, i.e. such a result would occur by chance only once in a hundred times) accepted as convincing.

Procambial strand: strand of undifferentiated cells in young stem which develops into vascular bundle.

Procumbent stem: lying loosely on the surface of the ground.

Prostrate stem: lying fairly close to the ground.

Protandrous: stamens dehiscing before the stigmas are receptive.

Protogynous: stigmas receptive before the stamens dehisce.

Protophloem: first formed primary phloem.

Protoplasm: living material of the plant or animal.

Protoxylem: first formed primary xylem.

Pseudospikelet: part of inflorescence in bamboos, like spikelet but with additional leafy structures.

Pubescent: bearing short, soft hairs.

Pyxidium: a capsule which dehisces by a circular slit causing the upper part to form a cap which falls off.

Quern: primitive hand mill.

Raceme: inflorescence in which growth of single axis is continued, flowers being borne laterally.

Rachis: main axis of a grass or cereal spike, on which spikelets are borne.

Rachilla: axis of grass spikelet, on which florets are borne.

Radical: arising from soil-level.

Radicle: the embryo root in the seed.

Receptacle: the portion of the axis to which the floral parts are attached. Also used for the enlarged part of the peduncle to which the florets are attached in the *Compositae* and *Dipsacaceae.*

Recommended list: selected list including only those cultivars which have given good results in N.I.A.B. trials; usually revised annually.

Reflexed: turned sharply backwards or downwards.

Regular: symmetrical about more than one diameter (actinomorphic).

Reniform: kidney-shaped.

Reticulate: forming a network or having a network of surface ridges or markings.

Rhizomatous: having rhizomes.

Rhizome: underground more or less horizontal stem, usually thickened and perennial.

Root tuber or tuberous root: a short swollen root storing food.

Rotate corolla: flat, plate-like, not tubular or bell-shaped.

Rugose: having a wrinkled surface.

Runner: a long prostrate stem rooting at the apex and producing a new plant which later becomes detached from the parent.

Scarious: of leaves or bracts, thin dry membranous.

Schizocarp: a dry syncarpous fruit breaking up when ripe into one-seeded indehiscent portions.

Sclerenchyma: strengthening tissue with lignified cell walls.

Scur: short vestigial awn.

Secondary xylem and *secondary phloem:* produced from cells derived from the cambium.

sens. lat., *sensu lato:* in the broad sense.

sens. strict., *sensu stricto:* in the narrow sense.

Sepaloid: resembling sepals.

Sepals: the outer whorl of floral lobes, usually green.

Septicidal capsule: dehiscing along the partitions (septa).

Septum: a partition, e.g. the wall between neighbouring compartments of an ovary.

Sessile: not stalked.

Shrub: a short much-branched woody plant.

Sieve tubes: tubular cells with perforated transverse walls, present in the phloem and forming a longitudinal system for the translocation of elaborated foods.

Silicula: a short broad pod divided into two compartments by a thin septum and dehiscing when mature by the separation of the two valves formed by the pericarp.

Siliqua: a fruit similar to a silicula but long and narrow.

Simple: of a single piece, not compound.

Solitary flower or flower head: borne singly.

Sp: an abbreviation of *species* (plural Spp.).

Spathulate or *spatulate:* spatula-shaped, like the handle of a spoon.

Species: the main unit of plant classification; usually all plants which will cross freely to give fully fertile offspring are regarded as belonging to one species.

Spicule: small tooth or spine.

Spike: raceme in which florets (or spikelets) are sessile.

Spikelet: unit of inflorescence in *Gramineae,* consisting of (usually) two glumes at base and one to many florets borne distichously on rachilla.

Spine: a stiff sharply-pointed structure, a modified branch, petiole, stipule or peduncle.

Sporophyte: diploid generation, producing spores, alternating with gametophyte generation.

Staminate: having male parts (stamens) only.

Staminode: a rudimentary or imperfectly developed stamen.

Stellate: star-shaped.

Stigma: the part of the gynaecium which receives the pollen.

Stipules: outgrowths at the base of a leaf.

Stolon: more or less horizontal slender stem, usually above ground and then often rooting at the nodes; sometimes used of similar and short-lived stem below ground.

Stoloniferous: having stolons.

Stoma: aperture in epidermis, bounded by guard-cells.

Stomata: plural of stoma.

Style: a more or less elongated outgrowth of the gynaecium bearing the stigma.

Stylopodium: the enlarged base of a style; as in the *Umbelliferae.*

Sub-family: main division of a family; may include several tribes.

Subsp., *subspecies:* main division of a species; usually separated by geographical, ecological or genetic barriers.

Subulate: awl-shaped, narrowing from the base to a sharp point.

subvar., *subvarietas:* taxon below varietas but above forma.

Succulent: soft, thick and juicy.

Supernumary spikelets: extra spikelets occurring irregularly on spike.

Suture: the line of union of two parts; in fruits dehiscence may take place along a suture.

Sympodial: formed by several axes, cymose.

Syncarpous: consisting of two or more united carpels.

Syngamy: fusion of male and female gametes to form zygote.

Synonym: a name not accepted as the valid one.

Synthetic variety: one produced by bulking a number of distinct lines.

Tap-root: a well-developed vertical main root bearing lateral roots.

Taxon: a classificatory group of any size.

Taxonomy: the study of systematic classification.

Tendril: a slender organ which helps to support a plant by twining around neighbouring stems and other suitable objects. May be a modified stem, leaf or leaflet.

Tepal: perianth segment.

Terminal: at the end of, terminating.

Testa: the outer covering of a seed.

Tetraploid: with four sets of chromosomes.

Tetrarch: with four xylem groups.

Thorn: a modified shoot, leaf or part of a leaf which is woody and sharp-pointed.

Tiller: an axillary shoot formed without

stem elongation; used of cereals and grasses.

Tracheid: an elongated, lignified, water-conducting cell with pointed end walls (see xylem).

Translocation: the movement of elaborated substances within the plant.

Transpiration: the loss of water from the plant as vapour.

Transpiration stream: the upward passage of water and dissolved minerals through the xylem.

Triarch: with three xylem groups.

Tribe: a group of related genera within a family or sub-family.

Trifid: deeply divided into three.

Trifoliate: having three leaves or leaflets.

Triploid: with three sets of chromosomes.

Truncate: appearing to be cut off abruptly.

Tuber: a short, swollen underground stem storing food. See also *root tuber.*

Tunica: the outer part of a terminal meristem.

Unilocular: having one compartment only.

Unisexual: of one sex only.

var.: abbreviation of varietas.

Varietas: botanical taxon, smaller than subspecies and larger than subvarietas or forma; often anglicized as 'variety', or better as 'botanical variety', but this involves danger of confusion with next entry.

Variety: named form of a particular sort of crop plant; may be a clone if vegetatively propagated, a single genotype or a narrow range of genotypes if grown from seed: same as cultivar, which name should be used where any danger of confusion with preceding entry exists.

Vascular bundles: strands of food- and water-conducting tissue, containing xylem and phloem.

Viscid: sticky.

Versatile: with the anther so attached to the filament that it turns freely.

Vessels: tubular structures in plants in which water is translocated, part of the xylem.

Viviparous: producing living young; used of grasses in which spikelets are replaced by small leafy shoots.

Whorl: three or more structures of the same type arising at the same level.

Xenia: effect of foreign pollen; used where appearance of seed is altered by cross-pollination with different genotype.

Xerophyte: a plant adapted to dry conditions.

Xylem: wood; containing vessels and/or tracheids, fibres and xylem parenchyma.

Zygomorphic: not symmetrical about more than one diameter, irregular.

Zygote: the product of the union of two gametes.

DERIVATIONS OF PLANT NAMES

Gk. = Greek; Lat. = Latin

A. Names of Genera

Aegilops: classical name for a kind of wild oat.
Agave: Gk., noble.
Agropyron: Gk., field wheat.
Agrostis: Gk., field.
Aira: Gk. name for a grass.
Allium: Lat., garlic.
Alopecurus: Gk., fox tail.
Ammophila: Gk., sand-loving.
Ananas: from Peruvian name.
Andropogon: Gk., male beard.
Arrhenatherum: Gk., male awned.
Arum: a Gk. plant-name derived from the Arabic *ar,* fire; refers to the burning taste.
Arundinaria: named from *Arundo.*
Arundo: Lat., a reed.
Asparagus: old Gk. name.
Avena: old Lat. name.

Bambusa: from the Malayan name.
Bouteloua: (commemorative).
Brachypodium: Gk., short stalk.
Briza: Gk., *brizo,* to nod, refers to the movement of the panicles.
Bromus: Gk., food.

Calamagrostis: Gk., *calamas,* a reed, *agrostis,* a grass.
Chaetochloa: Gk., bristle grass.
Chloris: Gk., yellow-green.
Cocos: Span., grimace, from appearance husked nut.
Colchicum: Colchis on the Black Sea.
Cortaderia: (commemorative).
Crocus: the Gk. name.
Curcuma: Arabic, saffron.
Cynodon: Gk., dog tooth; may refer to the rows of tooth-like spikelets.
Cynosurus: Gk., dog's tail.

Dactylis: Gk., refers to fingers.
Danthonia: (commemorative).
Deschampsia: after Des Longchamps, a French naturalist.
Digitaria: Lat., finger.
Dioscorea: (commemorative).

Echinochloa: Gk., spiny grass.
Elaeis: Gk., *elaion,* oil.
Eleusine: town connected with Ceres.
Elymus: Gk., rolled up.

Festuca: ancient Lat. name for a blade of grass.

Gastridium: Gk., a small pouch.
Gladiolus: Lat., little sword.
Glyceria: from the Gk. for sweet.

Helictotrichon: Gk., coiled bristle.
Holcus: classical name for a grass.
Hordeum: old Lat. name for barley.
Hyacinthus: the Gk name.

Iris: Gk., the rainbow.

Juncus: Lat. *jungo,* to bind or tie, from the use for binding.

Koeleria: Koeler, a German botanist.

Leersia: after a German botanist, J. D. Leers (1727–74).

Lilium: classical name, perhaps from Celtic *li,* white.
Lolium: Lat. name for darnel.

Manihot: Brazilian name.
Milium: Lat., millet.
Molinia: Molina, a Chilean botanist.
Musa: named after the physician to the first Roman Emperor Octavius Augustus.

Narcissus: Gk. name perhaps from *narke,* numb.
Nardus: Gk. *nardos,* spikenard; the tufted growth resembles that plant.

Oryza: from the Arabic name.

Paspalum: Gk. name for some grass.
Panicum: old Lat. name.
Pennisetum: Lat., feather-bristle.
Phalaris: Gk. *phalaros,* shining; refers to the seeds.
Phleum: old Gk. name for some other plant.
Phragmites: Gk., hedge, from growth in boundary ditches.
Phormium: Gk., basket.
Poa: Gk., grass or fodder.
Psamma: from the Gk. for sand.
Pteridium: from the Gk. name for ferns.
Puccinellia: after Professor Puccinelli, an Italian botanist (1808–50).

Saccharum: Gk., sugar.
Sansevieria: (commemorative).
Secale: old Lat. name of some grain.
Setaria: Lat. *seta,* a bristle.
Sieglingia: named after Professor Siegling (1800).
Sorghum: from the Italian name.
Spartina: from the Gk. word for cord.
Sporobolus: Gk., seed throw.
Stipa: Gk., tow.

Triodia: Gk., three-toothed.
Trisetum: Lat., three bristles.
Triticum: Lat. name for wheat.
Tulipa: Turk. *tulband,* turban.

Vanilla: Span. *vainilla,* pod.
Vulpia: Lat. *vulpes,* fox, from the long awns.

Xanthosoma: Gk., yellow body.

Yucca: West Indian name.

Zea: old Gk. name for some other cereal.
Zingiber: Lat. ex Sanscrit, horn body.
Zizania: Gk., darnel.

B. Specific Names

Specific names are usually adjectives the gender of which agrees with that of the generic name. Thus, in association with different generic names, we may have *sativus,* masculine, *sativa,* feminine, and *sativum,* neuter; *arvensis,* masculine or feminine, and *arvense,* neuter; *ruber,* masculine, *rubra,* feminine, and *rubrum,* neuter. Adjectives ending in *-ens,* such as *procumbens,* remain the same in each gender.

Where substantive names (nouns) are used, they are given their own termination, e.g. *Achillea millefolium.* Such names were formerly printed with an initial capital, thus, *Achillea Millefolium, Allium Cepa,* etc. They are often old generic names.

abyssinicus: of Ethiopia.
aegilopoides: like *Aegilops.*
aestivus: summer.
agrestis: rural, rustic.
agriocrithon: agrion, wild; *crith,* barley.
alatus: winged.
albus: white.
altaicus: of the Altai Mts., central Asia.
alterniflorus: alternate flowered.
americanus: American.
ampeloprasum: vine leek.
anceps: two-headed.

ancestralis: ancestral.
anglicus: English.
angustifolius: narrow-leaved.
annuus: annual.
aquaticus: of water.
arenarius: of sandy places.
arundinaceus: reed-like.
arvensis: growing in cultivated fields.
ascalonicus: of Ascalon, Palestine.
asper: rough, as with hairs or projections.
aureus: golden.
australis: southern.
barbadensis: of Barbados.
barbatus: bearded.
bertolonii: (commemorative).
bicolor: two-coloured.
boeoticus: of Boeotia, in Greece.
brevis: short.
bromoides: like *Bromus*.
bulbosus: bulbous.
byzantinus: of Byzantium, Istambul.

caeruleus: sky-blue.
caespitosus: tufted.
callosus: hard skinned.
canariensis: of the Canary Islands.
caninum: pertaining to dogs.
capillaris: fine as a hair.
cepa: Lat. for onion.
cerealis: cereal.
commutatus: changing or changed.
comosus: leafy.
compactus: compact, dense.
compressus: compressed, flattened.
cristatus: crested.
crus-galli: cock's leg.

dactyliferus: bearing fingers (i.e. dates).
dactylon: fingered.
decumbens: decumbent (see glossary).
deficiens: lacking.
dicoccus: with two grains or berries.
dilatatus: swollen.
distichus: in two ranks.
duriusculus: somewhat hard or rough.
durus: hard.

echinatus: prickly, bristly.
elatius: taller.
esculentus: edible.

fallax: false.
fatuus: foolish, simple, unsavoury, useless.
fistulosus: fistular, hollow-cylindrical.
flavescens: yellowish.
flexuosus: flexuose, wavy.
fluitans: floating.

gandavensis: of Ghent.
geniculatus: geniculate, jointed.
georgicus: of Georgia.
germanicus: German.
gesnerianus: (commemorative).
giganteus: giant.
glaberrimus: smoothest.
glaucus: blue-grey.
glomeratus: clumped, shaped like a ball.
guineensis: of Guinea.

halepensis: of Aleppo.
hexastichus: in six ranks.
hirtulus: small and hairy.
hybridus: hybrid.

indicus: of the Indies.
inermis: unarmed, without awns, thorns or spines.
infirmus: weak.
ispahanicus: of Isfahan.
italicus: Italian.

japonicus: of Japan.
junceiformis: rush-like.
junceus: rush-like.

lanatus: woolly.
loliaceus: *Lolium*-like.
longus: long.
longicuspis: with long points.
ludovicianus: of Louis.

magnus: great
major: greater.
maritimus: maritime, of the sea.
maximus: largest.
mays: from Cuban name.
medius: medium, intermediate.
miliaceus: like millet.
minor: smaller.
mollis: soft.
monococcus: with one grain or berry.

montanus: of the mountains.
multiflorus: many-flowered.
muralis: of walls, (or mouse-like).
murphyi: (commemorative).
myosuroides: like the tail of a mouse.

nemoralis: growing in woods or groves.
nodosus: having swollen nodes.
nuciferus: nut bearing.
nutans: nodding.

odoratus: aromatic, fragrant.
officinalis: officinal, used in medicine.
officinarum: of druggists.
orientalis: oriental, eastern.
oryzoides: like *Oryza,* rice.
ovinus: pertaining to sheep.

perennis: perennial.
persicus: of Persia.
pinnatus: pinnate.
planifolius: flat leaved.
poeticus: of poets.
polonicus: Polish.
polystichus: many ranked.
porrum: Lat. name for leek.
praecox: precocious, early.
pratensis: growing in meadows.
primulinus: Primula-like.
pseudo-narcissus: false, i.e. not the classical, narcissus.
pubescens: pubescent, downy.
pungens: pungent.
purpureus: purple.
pyramidalis: pyramidal.

remotus: remote (spikelets).
repens: creeping.
robustus: stout.
ruber: red.
rufipogon: red beard.

sagittifolius: with sagittate leaves, see glossary.
sagu: Malay name.
sanguinalis: blood-red.
sativus: cultivated.
schoenoprasum: Gk., rush-leek.
secalinus: rye-like.
segetalis: of corn fields.
setaceus: bristle-like.
sisalanus: from Sisal, in Central America.
spelta: ancient name for a wheat.
speltoides: like *Triticum spelta.*
sphaerococcus: round berried.
spontaneus: originating of itself.
squarrosus: spreading at the tips.
sterilis: sterile, infertile, useless.
stoloniferus: having stolons.
strictus: upright, erect, inflexible, tight.
strigosus: having stiff bristles.
sudanensis: of the Sudan.
supina: lying back.
sylvaticus: forest-loving.

tazetta: Ital., little cup.
temulentus: drunken.
tenax: firm.
tenuifolius: slender-leaved.
tenuis: slender.
textilis: related to textiles.
thaoudar: local name.
timopheevi: (commemorative).
townsendii: (commemorative).
trifurcatus: three-forked.
trivialis: common, ordinary.
tuberosus: having tubers.
turgidus: turgid, full.
turanicus: of Turania, central Asia.
typhoides: like *Typha,* reed-mace, bulrush.

unioloides: like *Uniola,* another genus of grasses.

vavilovi: after N. I. Vavilov, a Russian scientist (1886–1942).
ventricosus: bellied.
veris: true, genuine.
vernus: vernal, of the spring.
vineale: of vineyards.
viridis: green.
vulgaris: vulgar, common.

xiphioides: like *Iris xiphium.*
xiphium: Gk., sword.

zeocriton: Gk. *zea,* name of some cereal; *crith,* barley.

UNITS AND CONVERSION FACTORS

Metric units are used throughout this edition, but numerous other units are or have been used in agricultural and botanical literature, and the following notes are given for reference.

Within the metric system standard prefixes are used for fractions and multiples of basic units; the commoner ones are as follows.

Fractions (Latin prefixes)
10^{-1} (1/10) deci (d)
10^{-2} (1/100) centi (c)
10^{-3} (1/1 000) milli (m)
10^{-6} (1 millionth) micro (μ, mu)

Multiples (Greek prefixes)
10 deca (da)
10^{2} (100) hecto (h)
10^{3} (1 000) kilo (k)
10^{6} (1 million) mega (M)

Special metric units
1 litre (l) = 1 cubic decimetre (dm^3)
1 cubic centimetre (cc, cm^3) = 1 millilitre (ml)
1 are = 100 square metres (m^2); hence 1 hectare (ha) = 10 000 m^2
1 (metric) quintal = 100 kilograms (kg). Note that quintal originally meant hundredweight (*c.* 50 kg), a similar difference is retained in German where 1 Zentner = 50 kg, 1 Doppelzentner = 100 kg
1 micron (μ, mu) = 1 micrometre (μm) = 0·001 mm

In some European countries the comma is used instead of the decimal point.

Approximate conversion factors

LENGTH
1 inch (1 in, 1″) = 25·40 mm
1 foot (1 ft, 1′) = 304·8 mm
1 yard (1 yd) = 0·9144 m
1 chain = 22 yards = 20·117 m
1 link = 1/100 chain = 7·92 inches = 201 mm
1 rod (pole, perch) = $5\frac{1}{2}$ yards = 5·03 m
1 line = 1/12 inch = *c.* 2 mm

AREA
1 square inch (1 sq in, 1 in^2) = 645 mm^2
1 square foot (1 sq ft, 1 ft^2) = 929 cm^2
1 square yard (1 sq yd, 1 yd^2) = 0·836 m^2
1 rod (square measure) = $30\frac{1}{4}$ yd^2 = 25·29 m^2
40 rods = 1 rood = $\frac{1}{4}$ acre = 0·101 ha
1 acre = 4 840 yd^2 = 0·4047 ha

VOLUME *(British Imperial)*

Liquid measure
20 fluid ounces = 1 pint = 0·568 litres
1 gallon = 8 pints = $227\frac{1}{4}$ in^3 = 4·546 litres
(*1 United States gallon = 0·83 Imperial gallons = 3·77 litres*)

Dry measure, used for corn and seeds
1 bushel = 4 pecks = 8 gallons = 36·368 litres
1 quarter = 8 bushels = 2·91 hl

(*1 United States bushel = 0·97 Imperial bushels = 36·25 litres*)

(Bushels, being a volume measure, cannot be directly related to weight, but the usual convention was to take the bushel of wheat as 60 lb (*c.* 27 kg), of barley as 56 lb (*c.* 25 kg) and of oats as 50 lb (*c.* 23 kg).)

MASS (weight)

1 ounce (1 oz) = 28·35 g

1 pound (1 lb) = 16 oz = 0·4536 kg

1 hundredweight (1 cwt) = 112 lb = 50·80 kg

1 ton = 20 cwt = 2 240 lb = 1·016 tonne (t)

ENERGY AND POWER

1 kilocalorie (Calorie, physiological or medical calorie) = 1 000 calories = 4·187 kilojoules (kJ)

1 standard nutrition unit (1 SNU) = 1 million kilocalories =4 187 MJ

1 horsepower = *c.* 746 watts (W)

1 watt = 1 J per second

RATES

(Note that rates can be expressed in three ways: thus kg per ha can also be written as kg/ha or as kg ha^{-1}.)

1 oz/yd^2 = 33·91 g/m^2 = 339 kg/ha

1 lb/acre = 1·121 kg/ha

1 cwt/acre = 125·5 kg/ha; hence 1 fertilizer unit (1/100 cwt) per acre = 1·255 kg/ha

1 Imperial bushel per acre = very roughly, and depending on kind of grain, 60 kg/ha

1 pint/acre = *c.* 1·4 l/ha

Metabolizable energy concentration (MEC) = metabolizable energy (ME) per kg dry matter (DM) = approximately, for most feeds other than oil seeds, D-value/6·3 MJ per kg

INDEX

Names of plant parts and processes common to most crop plants are not normally indexed except at their first mention or where they are discussed in detail. Names of cultivars, where these are cited as examples, are not indexed; for cultivars the appropriate National List or current NIAB Classified List should be consulted. Latin names in brackets are synonyms.

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